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THE LAW OF GEMINATE SPECIES

PRESIDENT DAVID STARR JORDAN

Stanford University

In "Evolution and Animal Life," by Jordan and Kellogg (page 120), the following words are used:

> "Given any species, in any region, the nearest related species is not to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort or at least by a belt of country, the breadth of which gives the effect of a barrier."

Substituting the word "kind" for species in the above sentence, thus including geographical subspecies, or nascent species, as well as species clearly definable as such, Dr. J. A. Allen accepts this proposition as representing a general fact in the relations of the higher animals. To this generalization Dr. Allen, in a late number of *Science*, gives the name of "Jordan's Law." The present writer makes no claim to the discovery of this law. The language above quoted is his, but the idea is familiar to all students of geographical distribution and goes back to the master in that field, Moritz Wagner.

This law rests on the fact that the minor differences which separate species and subspecies among animals are due to some form of segregation or isolation. By some barrier or other the members of one group are prevented from interbreeding with those of another minor group or with the mass of the species. As a result, local peculiarities arise. "Migration holds species true, localiza-

tion lets them slip," or rather leaves them behind in the process of modification. The peculiarities of the parents in an isolated group become intensified by in and in breeding. They become modified in a continuous direction by the selection induced by the local environment. They are possibly changed in one way or another by germinal reactions from impact of environment. At last a new form is recognizable. And this new form is never coincident in its range with the parent species, or with any other closely cognate form, neither is it likely to be in some remote part of the earth. Whenever the range of two such forms overlaps in any degree, the fact seems to find an explanation in reinvasion on the part of one or both of the forms. The obvious immediate element in the formation of species is, therefore, isolation, and behind these are the factors of heredity, of variation, of selection, and others as yet more or less hypothetical involved in the effect of impact of environment on the germ cells themselves. The formation of breeds of sheep as noted by Jordan and Kellogg (p. 82), seems exactly parallel with the formation of species in nature. In like manner, the occasional development of breeds arising from the peculiarities of individuals is possibly parallel with the "mutations" of the evening primrose. Such breeds are the Ancon sheep in Connecticut and the blue-cap Wensleydale[1] sheep in Australia. The ontogenetic species—groups in which many individuals are simultaneously modified in the same way by like conditions of food or climate—show no permanence in heredity. Such forms, however strongly marked, should, therefore, have no permanent place in taxonomy. The recent studies of Mr. Beebe on the effects of moist air in giving dusky colors to birds serve to illustrate the impermanence of the groups or subspecies characterized by dark shades of color developed in regions of heavy rainfall.

It may also be noted in passing that one cause of the

[1] Blue Cap, a ram of Leicester-Teeswater parentage, having a blue shade on his head, was the progenitor of a breed having this peculiarity, known as the Wensleydale, in Australia.

potency of artificial selection among domesticated animals or cultivated plants is that such selection is always accompanied by segregation. The latter is taken for granted in discussions of this topic and hence its existence as a factor is usually overlooked. While poultry or pigeons can be rapidly and radically changed by artificial selection, in isolation, no process of selection without isolation is likely to have any permanent result. For example, we know no way of improving the breed of salmon, because the salmon we have selected for reproduction must be turned loose in the sea, where they are at once lost in the mass.

New forms of gold-fish and carp can be made easily in domestication, because these fishes can be kept in aquaria or in little ponds, but new forms of mackerel or herring are beyond the control of man and the species actually existing have been of the slowest creation, their origin lost in geologic times.

One of the most interesting features of "Jordan's law" is the existence of what I may term *geminate* species—twin species—each one representing the other on opposite sides of some form of barrier. In a general way, these geminate species agree with each other in all the respects which usually distinguish species within the same genus. They differ in minor regards, characters which we may safely suppose to be of later origin than the ordinary specific characters in their group. Illustrations of geminate species of birds, of mammals, of fishes, of reptiles, of snails, or of insects, are well known to all students of these groups, and illustrations may be found at every hand.

Each island of the West Indies, which is well separated from its neighbors, has its own form of golden warbler. Each island in the East Indies has its geminate forms of reptiles or fishes. Each island of the Hawaiian group has its own representative of each one of the types or genera of Drepanidæ. Each group of rookeries in Bering Sea has its own species of fur seal.

One of the most remarkable cases of geminate species

is that of the fishes on the two sides of the isthmus of Panama. Living under essentially the same conditions, but separated since the end of the Miocene Period by the rise of the isthmus, we find species after species which has been thus split into two. These geminate species, a hundred or more pairs in number, were at first regarded as identical on the two shores of the isthmus. Later one pair after another was split into recognizable species. The latest authority on the subject, Mr. C. T. Regan, seems to doubt if any species of shore fishes are actually identical on the two sides of the isthmus.

To make this clear, though at the risk of being tedious, I give below a partial list of these geminate species about the isthmus of Panama:

Atlantic Coast	Pacific Coast
Harengula humeralis	*Harengula thrissina*
Clupanodon oglinus	*Clupanodon libertatis*
Centropomus undecimalis	*Centropomus viridis*
Centropomus pedimacula	*Centropomus medius*
Centropomus affinis	*Centropomus ensiferus*
Epinephelus adscensionis	*Epinephelus analogus*
Alphestes afer	*Alphestes multiguttatus*
Dermatolepis inermis	*Dermatolepis punctatus*
Hypoplectrus unicolor	*Hypoplectrus lamprurus*
Lutianus cyanopterus	*Lutianus novemfasciatus*
Lutianus apodus	*Lutianus argentiventris*
Lutianus analis	*Lutianus colorado*
Lutianus synagris	*Lutianus guttatus*
Hæmulon album	*Hæmulon sexfasciatum*
Hæmulon parra	*Hæmulon scudderi*
Hæmulon schrancki	*Hæmulon steindachneri*
Anisotremus suriamensis	*Anisotremus interruptus*
Anisotremus virginicus	*Anisotremus tæniatus*
Conodon nobilis	*Conodon serrifer*
Pomadasis crocro	*Pomadasis branicki*
Calamus macrops	*Calamus taurinus*
Xystæma cinereum	*Xystæma simillimum*
Encinostomus pseudogula	*Encinostomus dowi*
Kyphosus incisor	*Kyphosus analogus*
Isopisthus parvipinnis	*Isopisthus remifer*
Nebris microps	*Nebris zestus*
Larimus fasciatus	*Larimus pacificus*

Atlantic Coast	Pacific Coast
Odontoscion dentex	*Odontoscion xanthops*
Corvula sialis	*Corvula macrops*
Bairdiella veræ-crucis	*Bairdiella armata*
Micropogon furnieri	*Micropogon ectenes*
Umbrina broussoneti	*Umbrina xanti*
Menticirrhus littoralis	*Menticirrhus elongatus*
Eques acuminatus	*Eques viola*

This list may be greatly extended, but the series noted will illustrate the point in question. Whenever a distinct and sharply defined barrier exists, geminate or twin species may be found on the two sides of it, unless, as sometimes happens, the species has failed to maintain itself on one side of the barrier. So far as Panama is concerned, we have evidence that the barrier was raised near the end of Miocene time with no trace of subsequent depression. We can thus form some estimate of the age of separation in at least a small number of closely related species. In this and similar cases it is not possible to conceive of the formation of these species by sudden mutation, or that they would retain their separate existence were the element of segregation removed. While segregation or isolation is not a force, and perhaps not strictly a cause in species formation, it is a factor which apparently can never be absent, if the species retains its independent existence.

There is no doubt that the distribution of higher animals in general is in accord with "Jordan's Law." Examples by the thousand come up from every hand. If we had a hundredth part of the amount of available evidence in support of mutation theories, these theories would pass from the realm of hypothesis into that of fact. But the application of this law or rule to plants and to one-celled animals has been questioned. So far as rhizopods are concerned, Dr. Kofoid finds that the species are in general sharply defined and of the widest distribution in the sea, so that we can hardly state laws as defining their geographical distribution. To these minute floating animals, the sea scarcely offers barriers at all, and the recognized species do not seem to be products of geographical iso-

lation. Doubtless these species in duration and in nature correspond more nearly to genera or families of higher animals than to actual species. Perhaps minor specific differences such as we note among arthropods or vertebrates are intangible or non-existent. The effects of isolation may be tangible only among forms which possess more varied relations with their environment.

The application of this law to plants has also been denied. But geminate species are just as common in botany as in zoology, and the effects of isolation in species-forming are just as distinct. The law is just as patent in the one case as in the other. It is merely obscured by other laws or conditions which obtain among plants.

In the nature of things, most physical barriers are more easily crossed by plants than by animals. The possibilities of reinvasion are thus doubtless much increased. The plant is limited by climate, rainfall, nature of soil, and the same species is likely to occupy all suitable locations within a large area. Animals are more mobile than plants within their range, a fact which tends to keep the interbreeding masses more uniform. In the struggle for existence, the plant is pitted against its environment. Whether a plant survives or not depends not much on the nature of the seed, but mainly on its relation to the spot on which it falls. There is little selection within the species due to the choice of one individual as against another. This can only happen where plants are overcrowded, and there the survival is mainly that of the seed whose roots run deepest. There is little room for struggle between closely related species. Each individual grows—if it can—on the spot where it falls. The variations among plants are great, but these variations are mostly lost unless reinforced by segregation. There is no likelihood of the survival of DeVries' mutants of the evening primrose if these forms are left free to mix in the same field.

Among plants we often notice the fact—rare though not unknown among animals—of numerous species of the same genus occupying the same area. In some cases these

species are closely related, suggesting mutants, and in other cases the relation indicates the existence of hybrids. In California, for example, there are in the same general region many species of Lupinus, of Calochortus, of Ceanothus, of Arctostaphylos, of Eschscholtzia, of Godetia, of Œnothera, and Opuntia. Eucalyptus, Acacia and Epacris in Australia are examples even more striking. But I have never seen very closely related or geminate forms in any of these genera actually growing together. I suspect that they do so sometimes and that the explanation is found in reinvasion. But "growing together" is an indefinite statement as applied to plants. The elder, the alder and the madroño (arbutus) abound in the Santa Clara Valley. But no one ever saw any two of these trees standing side by side. Each has its limitations, as to soil and moisture.

Setting aside these genera which are represented by many species in a limited area, and among which mutation and hybridism may be conceivably factors in species-forming, we find the law of geminate species applying to plants as well as to animals. Crossing the temperate zone anywhere on east and west lines, we find species after species replaced across the barriers by closely related forms. Illustrations may be taken anywhere among the higher plants—equally well, no doubt, among lower ones. Many genera are local in their distribution, monotypic—with a single species, the origin of which can not be traced. But many other genera belt the earth or come very near doing so, each form or species being geminate as related to its next neighbor. This fact is illustrated in Rubus, Alnus, Sambucus, Platanus, Fagus, Veratrum, Symplocarpus, Symphoricarpus, Castanea, Quercus, Pinus, Tsuga, Acer, Rhus, Pyrus, Prunus, Lonicera, Ranunculus, Trientalis, Lilium, Trillium, Veronica, Aquilegia, Gentiana, Viola, Epilobium, Pteris, Mimulus, Trifolium, Solidago, Aster. All these genera and many others furnish an abundance of examples.

We may, therefore, say that with plants as well as animals geminate species as above defined owe their dis-

tinctness to some form of isolation or segregation, and that, broadly speaking, with occasional exceptions, given any form of animal or plant in any region, the nearest related form is not to be found in the same region nor in a remote region, but in a neighboring region, separated from the first by a barrier of some sort, not freely traversable.

A law, that is, an observed relation of cause and effect is not invalidated by the presence of other effects due to other causes, in the same environment. The actual conditions in nature are everywhere not products of single and simple forces, but resultants of many causative influences, often operative through the long course of the ages.

It may be urged that these geminate groups or forms are not true species, because they often intergrade one into another, and they would probably be lost by intermingling if the barriers were removed. It is sometimes claimed that only physiological tests of species can be trusted, as true species will not blend and their hybrids, if formed, will be sterile. All this is purely hypothetical and impracticable to the systematic zoologist, and not of much value to the botanist. Closely related species can usually be readily crossed. As the relation becomes less close, partial sterility of all grades and then total sterility appear.

Species as we find them in nature are real *species* if that term has any definition. And real species have, as a rule, indefinite boundaries, shading off into subspecies, geminate species, ontogenetic forms and the like. And if we are to understand the significance of nature, we have to describe these facts and relations as they actually are. Then we have to find out what changes we can work in individuals and in species by such alterations of conditions as experiment can give.

We do not know actually any species of animal or plant until we know all changes that would take place in its individuals under all conditions of environment.

FASCIATIONS OF KNOWN CAUSATION

DR. HENRI HUS

MISSOURI BOTANICAL GARDEN

AMONG plants, whether in the garden or in the field, individuals occur with greater or less frequency, which, because they exhibit a striking departure from the accustomed form, attract immediate attention. To denote such abnormal forms, the term "teratological" is used. Teratology covers a wide field. It includes the deviations from the usual arrangement of the parts, such as the union of organs and alterations of position, as well as deviations from the form, number and size of the parts of the plant. Frequently an explanation does not readily offer itself, at other times the inciting cause is demonstrated without trouble.

Though it is only in comparatively recent years that the true value of the study of abnormal forms has been realized, it must not be thought that in the earlier days the subject was overlooked. Numerous papers on teratological cases were published during the seventeenth century, for instance that by Wurffbain.[1] The eighteenth century saw an increase in the number of similar publications. Even Linnæus, before he enunciated his "varietates levissimas non curat botanicus," seems to have devoted some time to the study of abnormal forms.[2] At the same time, it was not until 1814 that the first collective publication on this subject, covering more than 300 pages and containing several illustrations, appeared.[3] This, at greater or lesser intervals, was followed by others, the

[1] Wurffbain, Johannes Paulus. De folia lactucæ monstroso. "Miscell. Acad. Nat. Curios.," Dec. 2, A. 10, 411, 1691.

[2] Linnæus, Carolus. Pommerantz med et inneslutit foster. "Vetensk. Akad. Handl.," A. 281, 1745.

[3] Jaeger, G. F. Ueber die Missbildungen der Gewächse. Stuttgart, 1814.

most important being those of Schlotterbeck,[4] Engelmann[5] and Moquin-Tandon.[6] Since the middle of the last century numerous smaller papers on teratological subjects have appeared. The earlier data have been collected by Masters[7] and by Penzig,[8] in the former publication the abnormalities being arranged according to kind, in the latter under the various families, genera and species.

The main point of interest in abnormal forms lies not in the mere fact of the existence of the abnormalities nor in the extremes which they may reach, but rather in the light thrown by them upon plant development,[9] and they are therefore entitled to equal consideration with hybridization[10] which, as de Vries[11] has pointed out, permits the analysis of the specific characters and thereby makes possible the study of a single character, since the plant is to be considered merely as an expression of the reaction of elementary units, sometimes occurring singly, at other times in groups.

Among the plant monstrosities which are most frequently observed are fasciations, in which more often the stems, but sometimes other parts of the plant, appear to broaden and assume a flat appearance. Their existence has been known for centuries, for instance the fasciation of *Sedum reflexum* (*S. crispum*), illustrated by Munting[12]

[4] Schlotterbeck, P. J. Schediasma botanicum de monstris plantarum quo analogiam regno vegetabili cum animali intercedentem in producendis iisdem adstruit et figuris illustrat. *Acta Helvetica*, 2: 1, 1816.

[5] Engelmann, G. De Antholysi Prodromus. Frankfurt a. M., 1832.

[6] Moquin-Tandon, A. Éléments de Tératologie Végétale. Paris, 1841.

[7] Masters, M. T. Vegetable Teratology, London, 1869.

[8] Penzig, O. Pflanzen Teratologie. Genua, 1890–1894.

[9] Goebel, K. Bedeutung der Missbildungen für die Theorie der Organbildung. Organographie der Pflanzen, 173, 1898–1901.

[10] Tschermak, E. The Importance of Hybridization in the Study of Descent. Report of the Third International Conference on Genetics. Royal Horticultural Society, 278–284, 1906.

[11] de Vries, Hugo. Intracellulare Pangenesis. Jena, 1889. Sur les unités des charactères spécifiques et leur application a l'étude des hybrides. *Rev. gén. bot.*, 12: 257, 1900.

[12] Munting, A. Waare Oeffeninge der Planten, 1672.

and in numerous species, in fact, in so many species, in so many genera and in so many families, among fungi, among gymnosperms, among monocotyledons and dicotyledons, on herbs, on shrubs and on trees, that the assumption appears justified that fasciation may be expected to make its appearance at some time, in some part, in any species. This is the view held by Sorauer,[13] but de Vries[14] does not make so sweeping a statement.

Fasciations may be propagated vegetatively, for instance, by means of tubers, as in *Oxalis crenata*[15] or through cuttings, as was done at the Missouri Botanical Garden for fasciations of the tomato, *Solanum Lycopersicum*, snap-dragon, *Antirrhinum majus*, hen-and-chickens, *Echeveria glauca* and others. Fasciations may also be transmitted through seed. Among the best known instances is the cockscomb, *Celosia cristata* and its varieties, which, because of this abnormality, is cultivated in gardens. It is a form which, like the cockscomb amaranth, *Amaranthus cristatus*, has been known for centuries to exist, and is always propagated through seed. Recently it has again been shown for Munting's *Sedum reflexum*[16] as previously by de Vries.[17]

The possibility of the transmission of the fasciated character to the offspring, had already been recognized by Godron[18] who, however, says: "Les fasciés sont rarement héréditaires et jamais d'une manière absolue." While the truth of the latter part of the statement has been borne out by subsequent work, in the light of experiments carried on during the last twenty years, and especially those of de Vries,[19] the first part should be amended.

[13] Sorauer, P. Handbuch der Pflanzen-krankheiten, 1[3]: 334, 1906. "Die Fähigkeit zur Fasciation ist bei allen Pflanzen voraus zu setzen."

[14] De Vries, Hugo. Die Mutationstheorie, 2: 551. Leipzig, 1901–1903.

[15] 17th Ann. Rep. Missouri Botanical Garden, 147, 1906.

[16] Von Wettstein, R. Die Erblichkeit der Merkmale von Knospenmutationen. Festschrift zu P. Ascherson's Siebzigstem Geburtstage, 509, 1904.

[17] Mutationstheorie, 1: 128.

[18] Godron, A. Mélanges de Tératologie Végétale. *Mém. Soc. d. Sc. Nat. d. Cherbourg*, 16: 97, 1871–1872.

[19] De Vries, Hugo. Over de erfelykheid der fasciatien. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa*, 6: 72, 1894.

We have a right to believe that fasciations, like other monstrosities, with the exception, perhaps, of some cases of virescence,[20] may be inherited, though not by all descendants. Else such varieties could not be offered on the exchange list of the Amsterdam botanic garden as *Aster Tripolium fasciatum, Geranium molle fasciatum, Picris hieracoides fasciata, Veronica longifolia fasciata* along with *Chrysanthemum segetum fistulosum,* in which the ligulate florets have become tubular like the disk flowers, *Dipsacus sylvestris torsus,* which has a twisted stem, *Lychnis vespertina glabra,* which lacks the trichomes on the pod, etc.[21] But it must be remembered that good soil, great care, especially in the earlier stages, plenty of room—in one word, optimum conditions only—give the desired result.

Of far greater interest, at the present time at least, is the consideration of the causes of fasciation and its exact nature. Two kinds of fasciation appear to be possible. The one is caused by the combination, in a plane, of several axes, according to Lopriore.[22] The other mode of fasciation, far more common, and the one which will be considered here, consists of the flattening of the stem through a broadening of its apical cone into a comb, as shown by Nestler,[23] who did his work at the laboratory

[20] De Vries, Hugo. Een epidemie van vergroeningen. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa,* 8: 66. 1896.

In at least one case, that of the green-flowered *Oxalis stricta,* it has been shown that virescence may be transmitted through the seed (18th Ann. Rep. Missouri Botanical Garden, 99, 1907). The third observed, generation of these plants, now (January, 1908) in flower in the greenhouse, still shows the typical character. Now, as formerly, there is no sign of insects to which the cause of the virescence could be attributed.

[21] De Vries, Hugo. Erfelyke monstrositeiten in den ruilhandel der botanische tuinen. Avec un résumé en langue française. *Bot. Jaarb. Dodonæa,* 9: 62, 1897.

[22] Lopriore, G. I caratteri anatomici delli radici nastriforme. Ex. in *Zeitschr. f. Pflanzenkr.,* 14: 226, 1904.

"Solche bandförmige Nebenwurzeln entstehen entweder durch dichtes Aneinanderschlieszen mehrerer senkrecht übereinanderstehenden zylindrischen, oder durch gleichsinnige Verwachsung der Zentralzylinder mehrerer Seitenwurzeln, die sich mit einer gemeinsamen Rinde umgeben."

[23] Nestler, A. Untersuchungen über Fasciationen. *Oester. Bot. Zeitschr.,* 44: 343, 1894.

for plant physiology at Amsterdam under the direction of de Vries. That we are dealing with but a single branch, and not several, though frequently the ribbed appearance of a fasciation gives cause to think otherwise, is well shown by Sorauer[24] in the case of a fasciation of the Norway spruce, *Picea excelsa.* It is demonstrated first of all by the position of the leaves, which are arranged in continuous spirals, and further by the cross sections of the fasciation at different points. They all show the vascular bundles and the pith arranged as a single, continuous mass, and not as a combination of a number of adjacent rings, which would have been the case had the fasciation resulted through the union of various originally distinct branches.

For the sake of convenience in discussion, the causes of malformations in general and fasciation in particular will be considered under four heads: (1) Mechanical action, brought about by the elements, man or other vertebrates; (2) cases where no injury can be traced; (3) the action of fungi; and (4) the action of insects.

Traumatisms appear, in the majority of cases, to be the inciting causes of the appearance of teratological characters. Numerous instances of this are to be found throughout our literature. Blarighem[25] found that in the case of the pansy, *Viola tricolor* var. *maxima,* it was caused by an accidental crushing of a young shoot. Similarly, he has been able to constatate[26] that in clover fields which had been mowed twice, the number of individuals of red clover, *Trifolium pratense,* bearing 4–5-foliate leaves, was from 12 to 37 per hundred, while in fields which never had been cut, but 5 to 8 such plants were found per thousand. Sainfoin, *Onobrychis sativa,* under the same conditions, produced in its pinnate leaf, leaflets grouped in threes and fours. Plants of the ox-eye daisy, *Leucanthemum*

[24] *Ibid.,* 333.

[25] Blarighem, L. Production par traumatisme d'anomalies florales dont certaines sont héréditaires. *Bull. Mus. d'Hist. Nat.,* 10: 399, 1904.

[26] Blarighem, L. Anomalies héréditaires provoqués par les traumatismes. *Compt. Rend. Acad. Sc.,* 140: 378, 1905.

vulgare (*Chrysanthemum leucanthemum*), of which the stems had been cut, bore heads on which at least a part of the ligulate flowers had been changed to tubular flowers, as well as heads, which in the axils of the bracts, bore secondary ligulate florets. Life[27] mentions the case of a plant of *Ambrosia artemisiæfolia* which, having been run over by a wagon and badly injured in consequence, bore both staminate and pistillate flowers in an abnormal condition. A hedge composed of plants of *Cereus margi-*

"ROSA DE ORGANO"—*Cereus marginatus*.

natus, which, under the name Organo, is largely used as a hedge plant in Mexico, which was partly injured, probably because of securing cuttings for planting, shows numerous fasciations.[28] Klebs[29] mentions the observations of Krasan, who noted fasciation caused by a loss of leaves through the action of june bugs or spring frosts.

[27] Life, A. C. An Abnormal Ambrosia. *Bot. Gaz.*, 38: 383, 1904.

[28] A photograph, by Professor Frederick Starr (reproduced here), illustrating a large portion of a hedge thus fasciated, and a cast of one of the branches, are in the herbarium of the Missouri Botanical Garden. See also *Trans. Acad. Sc. St. Louis*, 9: xx, 1899.

[29] Klebs, G. Ueber künstliche Metamorphosen. *Abh. naturf. Gesell. Halle*, 25: 134, 1903–1906.

It is but natural to suppose that if accidental mechanical injury can produce abnormalities, the same can be produced experimentally through similar action. Again, numerous cases are on record. The first instance known is probably the experiment of Sachs,[30] who, amputating the main stem of bean seedlings just above the cotyledons, was able to bring about fasciation of the shoots produced from the buds in the axils of the cotyledons. A fasciation of *Ibervillea sonoræ* at the New York Botanical Garden, referred to in *Torreya*,[31] is understood to have been artificially caused by intentional slight injury of the growing tip. Blarighem[32] was able to cause fasciation of shoots of *Viola tricolor* var. *maxima* by crushing the young stems. Lopriore,[33] incited by the experiments of Sachs, cut the root tips of seedlings of *Vicia Faba* and obtained fasciated roots in a large number of cases, as well as malformations of other parts of the plant.

But apparently a fasciation is not necessarily a consequence of mutilation. Goebel[34] mentions fasciations in suckers and watersprouts. These are so common that they probably have come within every one's notice. Fasciations also frequently occur in plants the seedlings of which were abnormal in having a larger number of cotyledons than usual.[35] It has been shown[36] that under proper conditions of moisture and food, plants will frequently fasciate, though adjacent plants may remain normal. Such cases have generally been ascribed to peculiar conditions of nutrition.

[30] Sachs, J. Physiologische Versuche über die Keimung der Schminkbohne (*Phaseolus multiflorus*). *Sitzungsber. d. k. k. Akad. d. Wiss. in Wien*, 37: 57, 1859.

[31] Knox, Alice A. Fasciations in *Drosera, Ibervillea,* and *Cecropia. Torreya*, 7^5: 102.

[32] *Loc. cit.*

[33] Lopriore, G. Verbänderung infolge des Köpfens. *Ber. d. d. Bot. Ges.*, 22: 304, 1904.

[34] Goebel, K. Organographie der Pflanzen, 164, 1898–1901.

[35] De Vries, Hugo. Eine Methode, Zwangsdrehungen aufzusuchen. *Ber. d. d. Bot. Ges.*, 12^2: 25, 1894.

[36] 17th Ann. Rep. Missouri Botanical Garden, 147, 1906.

That parasitic fungi are able to produce an alteration of form in plants has long been known. One of the most familiar abnormal growths from such a cause is what is commonly termed a witch's broom, so often observed on evergreens. It is due to the action of species of Exoascus and Æcidum, which induce the formation of a large number of adventitious buds within a comparatively short area of the stem or branch, which give rise to a corresponding number of short, thickened twigs. In the silver fir, *Abies pectinata,* witches brooms are produced by *Æcidium elatinum.*[37] Frequently galls are produced by fungi, affecting either roots, stems or leaves, but no cases are on record where a fungus was shown to be the cause of fasciation. This is different where gall-insects are concerned. Here some cases have been traced directly to gall-insects[38] as the cause.

Galls, otherwise known as cecidia, and distinguished according to their origin into zoo- and phytocecidia, are among the most interesting of the abnormal forms which from time to time make their appearance as excrescences of widely varying shape, color and structure. Recognized by Pliny, some were even in those early days used in medicine because of their astringent properties. To-day, a number of them, especially some occurring on certain species of Quercus, Pistacia, Rhus and Tamarix, are of economic value[39] on account of their tannin content, and a gall produced by *Cynips tinctoria* upon branches of the dyer's oak, *Quercus lusitanica* (*Q. infectoria*), found in the countries bordering the Mediterranean and in the Orient, is official in the U. S. Pharmacopœia. Members of widely different orders of insects may be the cause of the

[37] Kerner, A., and Oliver, F. W. The Natural History of Plants, 2: 527, London, 1894–5.

[38] Though gall insects only are discussed here it does not follow that larvæ of other insects may not be the cause of fasciation. The relation between fasciation in species of Œnothera and the larvæ of a small moth, Mompha, is discussed in a very interesting, well illustrated paper by Knox, *The Plant World,* 10^7: 145.

[39] Wiesner, J. Die Rohstoffe des Pflanzenreiches, 1: 674, Leipzig, 1900.

production of a gall. Among the Arachnida, many of the mites do so, some species causing serious injuries; for instance, the pear leaf blister mite, *Eriophyes pyri,* and *E. oleivorus,* which causes the so-called "russet" oranges.[40]

To the Hemiptera, of which the plant-lice, Aphididæ, are best known, belongs the dreaded *Phylloxera vastatrix,* which some thirty years ago so seriously crippled the vineyards of France. It forms galls on both the leaves and the roots. The Diptera, to one of the families of which our common house fly belongs, yield the Cecidomyidæ. One of these very small insects is the cause of the goldenrod rose. Neither the Lepidoptera nor the Coleoptera have many members which are the cause of gall formation. This is different as far as the Hymenoptera are concerned. A large number of species, especially those belonging to the Cynipidæ, are the cause of the formation of some of the largest, most strikingly colored galls, of which those occurring on oaks (Cynips) and roses (Rhodites) are probably the most familiar.

In some cases the causation of fasciations has been ascribed to gall-forming animals. Kerner[41] speaks of the fasciations of the ash, *Fraxinus excelsior* and *F. ornus,* caused by a mite, Phytoptus (Eriophyes). De Vries[42] mentions a stem of *Hieracium vulgatum* attacked by *Aulax Hieracii* which was normal below the gall, but above it was fasciated. Not only fasciations, but numerous other monstrosities have been brought into relation with gall insects. Treub[43] observed virescence caused by the same insect. Nalepa[44] mentions *Phytoptus anthocoptes* as the cause of virescence of flowers, thickening of the capita and frequent secondary formation of capitula on *Cirsium*

[40] Cook, M. T. Insect galls of Indiana. Indiana Dep. of Geol. and Nat. Res., 29th Annual Report, 801, 1904.

[41] *Ibid.,* 2: 549.

[42] Mutationstheorie, 1: 291.

[43] Treub, M. Notice sur l'aigrette des Composées a propos d'une monstruosité de l'*Hieracium umbellatum. Arch. Neérl. d. sc. phys. et nat.,* 8: 1.

[44] Nalepa, A. Neue Arten der Gattung *Phytoptus* und *Cecidophyes. Denkschr. d. k. Acad. d. Wiss.,* 59: 525, 1892.

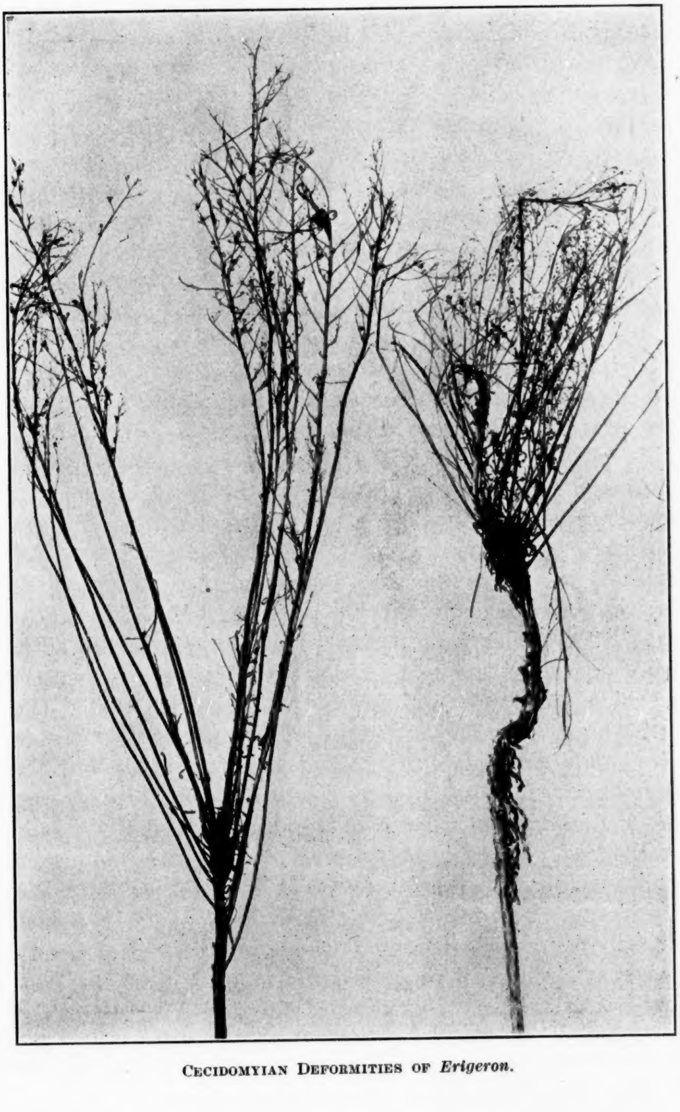
arvense, P. cladophthirus as the cause of gray-hirsute malformations of the shoots of *Solanum Dulcamara,* and *P. genistæ* as the cause of malformations of the tips of the shoots and abnormal hirsuteness of the buds of *Genista pilosa* and *Sarothamnus scoparius.* The virescence of the inflorescence of different species of Arabis, due to Aphides, was studied by Peyritsch.[45] De Vries[46] ascribes an epidemic of virescence among the plants in his experimental garden to an original infection caused by Phytoptus, though he was unable to demonstrate the presence of the mite. Finally Molliard[47] investigated the influence of fungi and insects causing floral cecidia upon the reproductive cells.

From the above it will be gathered that there exists a very definite relation between malformation in plants and gall-insects. For this reason a large number of strikingly abnormal plants of the horse-weed, *Erigeron canadensis,* growing within a narrowly circumscribed area in the immediate vicinity of St. Louis, Mo., attracted immediate attention and awakened considerable interest. Being found in January, nothing but the dried parts remained, which made observation easier. All of the plants were abnormal. Among them two distinct types could be distinguished. These types agreed in one particular. From the ground to a place 2½–3 feet above the soil, the plants were normal. It was above this point that the abnormality presented itself. In the first type, when the plant had reached a height of from 2½–3 feet above the ground it had evidently experienced a check. The main stem terminated here in a very much dried-up shoot but an inch or less in length, showing that it never had an opportunity to perfect its woody tissue. Just below this point numerous small side shoots occurred. These side

[45] Peyritsch, J. Zur Ætiologie der Chloranthien einiger Arabis Arten. *Jahr. f. Wiss. Bot.,* 13: 1, 1882.

[46] De Vries, Hugo. Een epidemie van vergroeningen. *Bot. Jaarb. Dodonæa,* 8: 66, 1896.

[47] Molliard, M. Recherches sur les Cécidies Florales. *Ann. d. Sc. nat. bot.,* 8. Sér., 1: 67, 1895.



CECIDOMYIAN DEFORMITIES OF *Erigeron*.

shoots had an average length of from 1½–2 feet, and, issuing within a space of 3 inches from the atrophied tip, gave the dried plant a peculiar broom-like appearance. Upon them, usually immediately at the base, frequently within 2 or 3 inches from the base and sometimes at a distance of one foot from the base of the side shoot, occurred elongated swellings, from ½–¾ inch long and increasing the thickness of the stem to three times its normal size. These also occurred on stems of the second type, which bore fasciations. Each of the swellings contained a single orange-colored larva, which Dr. M. T. Cook kindly determined as that of *Cecidomyia origeroni.* The species of Diptera, to which *Cecidomyia* belongs, lay their eggs on the surface of the plant, and the larvæ, after hatching, penetrate the tissues. In this they agree with the Arachnida and Hemiptera. The Hymenoptera puncture the tissues and deposit their eggs within the plant tissues. It has long been a question in exactly what manner the abnormal growth due to gall insects is caused. Some ascribe it to mere mechanical irritation on the part of the larvæ, others believe it to be due to a chemical stimulus emanating either from the parent insect, which, at least in some instances, deposits, along with the egg, a certain chemical substance, or from the young larvæ only.[48] The latter happens in the case of the gall caused by *Cecidomyia Poæ* upon *Poa nemoralis,*[49] and which brings about the formation of roots in places where normally they are never found. But when *Nematus Capreæ* makes a wound in the leaf tissue for the purpose of depositing an egg, a gall develops, whether an egg is laid or not. Even when the former has taken place, though the egg be subsequently destroyed, the gall develops just the same, though never attaining full size. For that matter, mere mechanical irritation, *i. e.,* the killing of one or a few cells at the

[48] Beyerinck, M. W. Beobachtungen über die ersten Entwickelungsphasen einiger Cynipidengallen, 177. *Veröffentlicht d. d. k. Acad. d. Wiss. zu Amsterdam,* 1882.

[49] Beyerinck, M. W. Die Galle von *Cecidomyia Poæ* an *Poa nemoralis. Bot. Zeit.,* 43^{20}: 304, 1885.

side of an organ, may result in the malformation of the adult organ, and, according to Ward,[50] may be proved experimentally by aid of a needle. But the assumption of a mere mechanical injury is not sufficient to account for the presence and shape of galls. The same insect, on different hosts, may produce different galls. Again, two distinct species of gall-insects produce very different galls on the same plant or even on the same leaf. Further, experiments to bring about artificially the formation of galls through the injection of different chemicals, have thus far proved unsuccessful.[51]

Among plants of *Erigeron canadensis* fasciation appears to be quite common.[52] When, however, among the plants of this fleabane infected by the Cecidomyia a large number, at least 10 per cent., were found to be fasciated, it was but natural to attempt to bring the two phenomena into relation. In some of these fasciated plants the fasciation begins within two feet of the ground; in others, and these form the majority, the fasciation began from 2½–3 feet above the soil surface and above the point where the galls occurred on the main stem. But while the non-fasciated plants showed a large number of long side shoots, developed at the expense of the main stem, the fasciated plants did not differ materially from normal plants in this regard. A large number of short side shoots bearing flowers were produced on a fasciated main stem. The most plausible explanation is that in the former case the growth of the main stem was inhibited absolutely and that all the strength went to form side shoots, while in the latter case the growing point was not affected sufficiently to dry up. Instead, growth was stimulated. Whether the action of the galls was of a mechanical or chemical nature, though of great interest in other cases, is of comparatively little importance here, and for the following reasons:

[50] Ward, H. Marshall. Disease in Plants, 131, London, 1901.

[51] Küstenmacher, M. Beiträge zur Kenntnis der Gallenbildungen mit Berücksichtigung des Gerbstoffes. *Jahrb. f. wiss. Bot.*, 26: 82, 1894.

[52] Penzig, *loc. cit.*

It has been conceded generally that fasciations are due to changed conditions of nutrition. Nestler, de Vries, Goebel, Sorauer and many others agree that they are induced either through an increase of nutrition of the entire plant or of that of certain shoots through the removal of others. In other words, it is due to a change of the chemical and physical conditions within the cell. The influence of chemical substances upon plant and animal cells has been widely studied. Among the best known are the experiments of Johannsen[53] in which lilac bushes and other flowering shrubs, of which we see the branches in the florist's windows in early spring, under proper conditions of moisture and temperature, were for a certain length of time exposed to the action of ether or chloroform, after which they bloomed several months earlier than normally would have been the case. Loeb's experiments on the cleavage of unfertilized eggs of the sea urchin, after having been treated with magnesium chloride, are too well known to make it necessary to go into detail. The same thing is true for his studies on the influence of the lack of oxygen and resultant modification in the cleavage of eggs of Echinodermata. Migula's experiments on the influence of dilute acid solutions on algal cells, Richards' work on the development of fungi under the influence of chemical stimuli, and especially the work of Sabline on the influence of external agents on the roots of *Vicia Faba* show that external influences may bring about profound nuclear changes. Still better, this is brought out by the injection experiments of MacDougal,[54] who was able to produce new species through the injection of dilute salt solutions into the capsules of evening primroses. And in the case of hyphæ of many of the Chytridiaceæ, which bring about abnormal cell divisions in the tissues of the host plant, the protoplasm of

[53] Johannsen, W. Das Aetherverfahren beim Frühtreiben, 2e Aufl., Jena, 1907.

[54] MacDougal, D. T., A. C. Vail and G. H. Shull. Mutations, Variations and Relationships of Œnotheras. Carnegie Institution of Washington Publication, No. 81, 1907.

the parasite never comes in direct contact with that of the host. Yet their influence extends to cells at some distance from the point of infection. Even where the hyphæ do not actually enter the cell, a stimulation to abnormal growth often takes place. Experimentally mere mechanical action has brought about profound changes. Molliard was able to induce the formation of double flowers through mechanical irritation.

That the action of galls is of a chemical nature is well shown by Molliard,[55] who describes and figures profound nuclear changes preceding the hypertrophy of *Geranium sanguineum* attacked by *Phytoptus Geranii.*

If fasciations, which are due directly to chemical changes within the cells, may be inherited, then why not galls? But acorns from an oak covered by galls produce normal plants only. Still, one might expect galls to be inherited in preference to fasciations. Does not de Vries[56] say: "It is clear that the beautiful, highly complex and judicious structure of the cynipid galls, with their food tissue, layers of stone cells, and the tannin-bearing, loose, outer parenchyma, in thickness adapted to the egg apparatus of the parasites and inquilinæ, can not be brought about by a mere mechanical stimulus." Kerner goes so far as to say that it is within the limits of possibility that the first double flowers were caused by some gall.

There is no direct evidence of the inheritance of abnormalities brought about through the influence of gall insects or their larvæ. Fasciation, however, from whatever cause, may be inherited by a greater or less percentage of the offspring. We may then assume there must be a predisposition to the formation of fasciation in all plants which up to this time have been known to produce them. Probably this disposition is present in all other plants. The assumption of a mere excess of nutrition is not

[55] Molliard, M. Hypertrophie pathologique des cellules végétales. *Rev. gén. bot.*, 9^{98}: 33, 1897.

[56] Mutationstheorie, 1: 290.

sufficient to explain the inheritance of the character. It is necessary to assume a corresponding and very definite change in the bearers of the hereditary characters. Just how these bearers are constituted or what name is given them is entirely immaterial. It is probable that they are of an exceedingly complex nature. For purposes of illustration they may well be compared with the molecules of organic chemistry, or better still, as has already been done so felicitously, to many-sided prisms, which a very slight jar causes to assume a different position and which finds a corresponding external expression. Under predisposition to fasciation or the latency of the fasciated character should perhaps be understood a tendency on the part of the cell contents, and more particularly the chromatin, to undergo a certain definite change, retained during cell division, of either a chemical or physical nature, under certain conditions brought about by differences in nutrition. The change which causes fasciation is one of the easiest brought about, and hence fasciation is one of the abnormal characters most frequently met with. Though a mere theory, its general truth is supported by a number of instances. Mutations frequently repeat themselves. The identical sports originating from stock obtained from widely different sources and where the probability of a common origin in the remote past may safely be questioned, speak for themselves. The finding in two distinct places in Europe of plants of *Capsella heegeri* Solms, which differs from *C. bursa-pastoris* mainly in the shape of its capsules, is another instance. Mutations in a species are always the same, whatever their direction. They may be widely separated in time and space, but whenever they appear they are identical.

It has been said that fasciations are inherited because the seeds collected for purposes of propagation always were obtained from the abnormal stems. This appears to have happened in the majority of cases. Since, however, we never can know whether a fasciation is inherited

or makes its appearance for the first time,[57] numerous experiments should be undertaken with a view of eliminating "chance" through large numbers. Whether the seed of a bean in which a fasciated root has been produced artificially, gives rise to a fasciated plant, is an experiment worth trying. Likewise, it is an open question whether the seed borne on normal stems of a pansy in the main stem of which fasciation has been induced through crushing, will give rise to fasciated individuals. The spores of the Boston fern, *Nephrolepis exaltata bostoniensis,* give rise to plants the majority of which exhibit the peculiar cristate leaves. Yet here and there on the fronds sometimes will be found non-cristate leaflets. Will the spores borne on the latter give rise to the cristate form? These are experiments which any one with a little space and time at his command and a penchant for gardening, can readily undertake. To such, no small hope of reward is held out in a recent paper by Blarighem,[58] who, as a result of mutilation, obtained entirely new and constant varieties.

[57] This is true even when it appears as a bud variation, for the character may have been latent in the parent plant. One can, therefore, not speak, in such a case, of an "acquired" character in the strictest sense.

[58] Blarighem, L. Action des traumatismes sur la variation et l'héridité. *Compt. Rend. hebd. d. Séanc. et Mém. de la Soc. de Biol.*, 57^2: 456, 1905.

THE AGGREGATE ORIGINATION OF PARASITIC PLANTS

DR. CHARLES A. WHITE

SMITHSONIAN INSTITUTION

IN the January number of THE NATURALIST I gave a review of the known phenogamous parasites, in which was discussed the relation of the parasites to one another, and to other abnormal plants; and the relation of all of them to normal plants. The present article is devoted mainly to the question of the manner of origination of the parasites as such, which, it is assumed, was by abnormal aggregate mutation from normal phenogams.

Parasitism in the animal kingdom is perpetrated by low, upon higher, forms of life, the parasites belonging to families, orders and even to classes, which are widely different from any of those which include the hosts. Parasitism of low forms of vegetable life upon higher forms is also everywhere prevalent, such as that of fungoid cryptogams upon phenogams, but the cases now under consideration are those of parasitism of various kinds of phenogamous plants upon other phenogams. Evidence of this phylogenetic relationship of parasites and their hosts, even in extreme cases of parasitic deformation, is fortunately preserved in that part of the structure of the parasites which pertains to parturital reproduction. That is, the florescence and fruitage of the parasites have remained characteristically phenogamous, each parasitic species having preserved at least those floral and pericarpal structures which normally characterize the phenogamous families, as such. It is thus observable that, in the abnormal mutation which produced the parasites, the effect was chiefly confined to the somatic parts of the respective plants and to those parts which are concerned in blastemal reproduction; while the parts immediately concerned in systematic genesis by parturital

reproduction were, at most, only slightly disturbed. So distinctly are the systematic characters of normal phenogams retained in the florescence and fruitage of the parasites that one seems forced to the conclusion that, in the great systematic development of vegetal forms, they all became phenogams before they became parasites. The phenogamous parasites, therefore, not only do not belong to a separate and predatory class, as is the case with other parasites, but they are depraved members of the same class, and sometimes of the same family, with their hosts. Still, their depravity is only with reference to the habits and structure of normal plants, for they all have great adaptability to their peculiar conditions, and their vegetal vigor is quite as great as is that of normal plants.

It is a fact worthy of special attention in this connection that although all the various forms of phenogamous parasitism are accompanied by greater or less abnormality of structure, they are in certain respects subject to the systematic restrictions which pertain to normal plants. That is, each form of parasitism affects not merely certain individual members of a given species, but every member of it; and the systematic limits of that species are, for itself, the limits of its own peculiar form of parasitism. Moreover, that form of parasitism which characterizes each of the different groups is shared without variation by every member of the group regardless of the generic or family relationship which it may bear to other plants. The habits and other parasitic characters of those depraved phenogams are as distinctly and permanently heritable as are the stated specific, and other systematic, characters of the same, or of any other, species, and there is no known evidence that any form of phenogamous parasitism has been derived by transmutation from any other parasitic form. Known evidence tends to show that every case of such parasitism originated independently of all other cases, and by a mutative process which imposed permanent abnormal characters

upon normal plants. Those abnormal characters all became connate with the normal characters after the establishment of their heredity, but they never became systematically correlated with them.

The questions that here almost crowd themselves upon one's attention are, how have those wayward phenogams accomplished their departures from normal conditions, and what was their incentive for doing so? Doubtless in all cases the chief incentive to parasitism, after the operation of an unknown predeterminate cause, has been food-lust, the instinctive object of the plant being to procure its nourishment in an immediately available form. The following respective references to the seven groups of phenogamous parasites are necessary to the present subject, but they show how difficult it is to make any sufficient answer to the first of those questions.

In pursuance of the subject as just indicated it may be suggested that the members of group I, which prey upon the roots of other plants and are only partially parasitic, originally acquired their habit of underground pilfering by the accidental chafing together of the tender roots of closely-growing plants, which brought bared, new-formed cells into contact at the crossings of the roots. Vital union of the roots at those points, such as takes place in grafting, having resulted, the more vigorous plant became the parasite by withdrawing a portion of the partly elaborated food-sap from the weaker one. It is plain, however, that thousands of cases are constantly occurring of similar contact of growing roots which do not result in parasitism. Both the normal and abnormal characters are possessed by every individual plant of every species pertaining to group I, and they are thus, all to the same extent, distinguished from normal plants and from all other parasites. In no case is one of this simplest of the forms of phenogamous parasitism known to show any inclination to greater complexity, or to abandon its present restricted parasitic habit. The heredity of that habit is permanent, and no known fact suggests that

it originated by any slow process, such as is generally understood to be the case in natural selection.

The mistletoes, which represent group II, have reached the condition of complete parasitism with less structural and functional change than have any of the other recognized groups. In view of the fact that they produce their own chlorophyl, and that their structure is very nearly normal, one can not doubt that they were originally normal phenogams, growing from the soil, although they will not now grow there. As a family also, they are now quite distinct from all other families, and as a group of parasites they are so clearly separate from every other group that one can not doubt that they have reached their parasitic condition in an entirely different manner. Their departure from the life-habit of normal phenogams evidently consisted only of the transference of germination and epitropism from the soil to the bark of trees; while the epitropic structure and functions, including both parturital and blastemal reproduction remained normal. Unnatural and lacking in apparent incentive as has been that transference, it is believed to have been suddenly accomplished for the whole family, no trace of transitional stages of parasitism having been discovered for the species of either the Old World or the New. Although the mistletoes are so nearly normal in structure, their parasitism is as complete and heritable as is that of any of the other groups.

The European species, *Lathræa squamaria,* which has been chosen to represent group III, besides being distinct from all other known parasitic forms, is, in a peculiar manner, suggestive of the assumed suddenness with which changes from normal to parasitic conditions have occurred among phenogams. This species has five distinct abnormal habitudes, which are repeated in succession in every individual plant. Its germination is from an ordinary seed in surface soil, and it is developed as a normal plantlet from a normal embryo; but it soon abandons itself to a remarkably diversified life. First, it produces

sessile haustoria upon some of its early roots and becomes partly parasitic in the same manner as do the members of group I, the structure and habit of which it then closely resembles. Second, it resorts bodily and suddenly to underground life by burrowing into the soil, where it becomes an intricate mass, often very large, of blanched stems and branches. Third, it abandons its early roots with their sessile haustoria, develops new pediculate haustoria from its underground stem and branches and becomes completely parasitic. Fourth, it changes some of its numerous aborted leaves into ingenious traps with which it captures minute animal forms and adds them to its other ill-gotten subsistence. Fifth, almost suggestive of atonement for a groveling life, it provides for the normal germination of its offspring by sending above ground a few specialized branches which produce perfect flowers and seed and then die, while the underground parts live perennially. That series of changes of structure and habitude within the life-history of a single plant has no known parallel in the vegetable kingdom. The changes have no apparent relevancy with one another until the closing one of the series, parturital reproduction, restores the normal phenogamous condition for a new reproductive cycle and a new series of the abnormal changes. All these changes of structure and habitude are invariable in character and invariably heritable. So far as is now known they are confined to a single species, and the structure of no other known plant offers any suggestion of their gradual origination. In view of such facts as these, all of which have been attested by competent observers, one may reasonably believe that not only this form, but all the forms of phenogamous parasites, have originated suddenly.

Although groups I, II and III are, by their respective methods of parasitism, clearly distinct from one another and from normal plants, parasitism is not physically manifested in any of them until after germination is completed, because the embryo of every member of each of

those groups is of normal structure. Every member of the four remaining groups, however, begins life in an embryo which is simple and filiform and without cotyledons, radicle and plumule, although the flower in which it is produced is of normal phenogamous structure. Moreover, although the simple abnormal embryo is physically identical for each of the four groups just mentioned, the resulting forms of parasitism are too widely different for each group to suggest for them even a remote community of origin.

A remarkable fact concerning group IV is that the two genera which compose it, Cuscuta and Cassytha, belong to widely different families, namely, Convolvulaceæ and Lauraceæ, respectively, and that the respective genera prevail in distantly separated parts of the world. Both genera are endowed with a single parasitic impress which distinguishes and dominates them equally in both habitude and somatic structure. That impress also separates all the species and individual plants of the whole group from normal plants and from all other parasites. The habits of this group, as shown by our well-known dodders, are widely different from those of all the other parasitic groups. They are all annual plants and consequently the whole life history of each species is crowded into a single season, which is shortened by late spring germination and early frosts. Therefore all the characteristics of the whole group lie dormant in the simple filiform embryo of every dodder seed for more than half of each year; and yet every one of those characteristics is invariably heritable and constant. Difficult as it is to understand how every individual member of such a distinctly defined double group of annual plants could have assumed their abnormal characteristics either slowly or suddenly, and attained a world-wide distribution, it is still more difficult to understand how two such diverse genera could have assumed identical parasitic characters. It is almost superfluous to add that the habits and structure of no known plant offers any suggestion of a gradual origina-

tion of the parasitic characters of group IV, or of the manner of its world-wide distribution.

As is the case with the other groups which are herein mentioned, nothing is known of the pre-germinative history of the characteristics of group V. The members of this group belong to a noted family of parasitic genera, the Orobancheæ, of which the destructive broom-rapes are among the best known examples. They all begin life in a simple, filiform embryo, which is not only without differentiation into cotyledons, radicle and plumule, but which is also extremely abnormal in its method of germination. The members of group V, like those of group IV, are annuals. As regards the structure of the seed and embryo and the initial conditions of germination, the members of both groups are similar, but their results are extremely different. The germinating offshoot of the former springs upward, sending no root into the ground, but seizing upon the growing parts of its companion plants by its haustoria. The offshoot of the latter burrows downward and seeks a root-host, failing to find which it dies without producing any upward growth. Finding a root-host, a substituent plantlet is developed from their conjoined parts which rises above ground, producing flowers and seed. The physical structure of the embryo of both plants is identical, and both are abnormal. Immediately upon germination the great differences between the plants appear, but neither in those differences or in their common embryonal structure is there any suggestion of a community of origin with each other, or with any other plants.

A leading characteristic of all the forms of phenogamous parasitism is the permanence and heredity of their attributes. Increasing abnormality of structure and habit, however, is suggested, but not proved, by the members of group VI, which is represented by the Rafflesias and some closely related genera. The conception which one naturally forms of a phenogam that may have been the normal ancestor of these plants is one having root, stem,

branches, leaves, flowers and fruit. These plants have discarded most of those essential parts, none of them having more than a short stem besides the fertile flower; and the sessile species, which are numerous, retain only the flower. Such a conception would therefore carry with it the idea that those eliminations were consecutively effected until the lowest structural limit was reached; but neither their own structure nor that of any other known plants affords the least indication that any of these parasites reached their present condition by either selective gradation of successive steps. The Rafflesias, like the mistletoes, are parasitic upon trees, and the seeds of both will not germinate successfully upon the ground. One may well believe that when the mistletoes abandoned the soil and inflicted themselves upon trees they took with them, and retained, all that they then needed for their support. But when the Rafflesias made their similar change, as they are assumed to have done, they required from their hosts the fullest possible tribute. Apparently sure of receiving it, they discarded as no longer necessary the principal part of their own somatic and blastemal structures, the sessile species retaining only those parts which are concerned in parturital reproduction, namely, only the flower. Their success has been complete, for although they are rootless, stemless, branchless and leafless plants, and originate from a structureless embryo, they are among the most vigorous of vegetable forms, the flower of the largest species sometimes reaching a diameter of more than three feet. One cannot conceive of a wider departure from normal conditions than is presented by group VI, or of a more complete isolation of structure and habit from all other plants.

Group VII, which is represented by the Balanophoreæ, is remarkable for the comparatively large number of systematic genera which it embraces, some of which are so greatly differentiated from others as to deserve recognition as sub-families. Some are comparatively inconspicuous; some produce large, showy flowers, and some

bear an outward resemblance to fungi, to which early botanists referred them. The genera of this group are still further distinguished by the comparatively small number of species which represent them, the average number to the genus being less than three. Yet all the members of this remarkably diversified group are developed from a simple filiform embryo by a germination similar to that of the broom-rapes, and all are rigidly controlled by one invariable and heritable method of parasitism. It is almost superfluous to add that there are no known intermediate forms between the parasitic species of this group, or between them and normal phenogams.

A leading purpose in the foregoing remarks is to express the belief and present evidence that all the various methods, or forms, of phenogamous parasitism have originated suddenly by abnormal mutation from normal phenogams and that each form originated independently of all the others. One can not doubt that, whatever may be the determinate cause, all mutations of plants, whether normal or abnormal, originated in changes of molecular conditions within the germ cell. Usually, those molecular changes are of phylogenetic character, but there is no reason to doubt that the changes which gave origin to the various parasitic attributes were also of like molecular origin. That is, referring to the theory of intracellular pangenesis of de Vries, each of those attributes, as well as their associated abnormalities of structure, both somatic and embryonic, had its origin in abnormal pangenes. Admitting such a community of molecular origin, there appears to be no more reason to doubt the origination of parasites by aggregate mutation than to doubt normal aggregate mutation.

One who accepts without qualification the theory of the origin of species by natural selection is no more likely to favor this idea of the sudden origination of the great and diverse groups of parasites which have been referred to in preceding paragraphs than he would be to accept the theory of special creation of species,

belief in which was formerly universally held. But by those who have given due consideration to paleontological facts with regard to the evidently sudden introduction at various stages of geological time, not merely of species, but orders and classes of animals and plants;[1] to the great array of facts presented by Professor Hugo DeVries in support of his mutation theory;[2] to the cases of aggregate mutation of Lycopersicum which I have published from time to time as results of my personal observations;[3] and to like cases of aggregate mutation of *Gossypium* which have been observed by Dr. O. F. Cook,[4] the proposition that the different forms of phenogamous parasitism have been introduced separately and suddenly will not be hastily rejected. When the attention of one who holds the former of the two views referred to is called to the cases of evidently sudden introduction of animal and vegetable forms during geological time he usually replies by deploring the imperfection of the geological record, although he constantly depends upon it in the multitude of cases in which phylogenetic continuity is evident. And yet, there is no break in the geological record, which is more abrupt and differential than is that which exists between the distinguishing characters of the phenogamous parasites and the normal characters of every other phenogam now living contemporaneously with them.

Briefly reviewing the foregoing subject, we find as follows: (1) The parasites which have been discussed are

[1] I have discussed these questions in Report of the Smithsonian Institution for 1901, pp. 631–640; *Bulletin Torrey Botanical Club*, New York, Vol. 29, pp. 511–522; Album der Naatur, Haarlem, April, 1903, pp. 231–238; Natur und Schule, Berlin and Leipzig, III Band, pp. 248–253; and *Science*, New York, Vol. XXII, n. s., pp. 105–113.

[2] Die Mutationstheorie, Leipzig, 1901.

[3] *Science*, n. s., Vol. XIV, pp. 841–844; *ibid.*, Vol. XVII, pp. 76–78. New York *Independent*, Oct. 16, 1902; *Bull. Torrey Bot. Club*, Vol. 29, pp. 511–522; *The Popular Science Monthly*, Vol. LXVII, June, 1905, pp. 151–161.

[4] *Proc. Washington Acad. Sci.*, Vol. VIII, p. 265; *Science*, n. s., XXVII, p. 193.

known to be phenogamous by the character of their florescence and fruitage, but for this occasion they are classified by their parasitic differences only. They are divided into no less than seven distinct groups, or kinds, which differ in character from root pilfering by means of a few haustoria to dominant rapacity, extreme deformation of somatic and embryonal structure and aberrant methods of germination. (2) The method of parasitism of each group is shared equally by every member of it, whatever may be the systematic affinities of the respective members, and the method of each group is entirely unlike that of every other group. (3) All the parasitic habits and structures are severally and completely heritable, and always connate with systematic features of the species in which they occur, but they are never systematically correlated with them. (4) None of the seven forms of parasitism shows any tendency to return to normal conditions, to become more complex, or to change from one form to another. (5) The normal florescence and fruitage of the parasites is assumed to indicate that they were originally derived from normal phenogams; but no trace of intermediate stages between even the most extreme cases of parasitism and normal plants has been discovered. The geographical distribution of all the known kinds of phenogamous parasitism, except that of group III, is almost world-wide. In consideration of these, and many kindred, facts it is assumed that the phenogamous parasites originated as such by sudden and aggregate mutation from normal phenogams, similar to, but not identical with, the phylogenetic aggregate mutation that has been observed in Lycopersicum and Gossypium.

THE EVOLUTION OF THE TERTIARY MAMMALS, AND THE IMPORTANCE OF THEIR MIGRATIONS[1]

PROFESSOR CHARLES DEPÉRET

University of Lyons

Note.—These very interesting and important papers by Charles Depéret, Dean of the Faculty of Science, University of Lyons, France, have been especially revised by the author (to date, November, 1907) before translation. The translation is the work of Miss Johanna Kroeber, graduate student of Columbia University. Dr. Charles R. Eastman of Harvard University and Dr. W. D. Matthew of the American Museum have kindly revised the translation. The correlation of the Tertiary of the Old and New World is of such commanding interest to paleontologists, zoologists and geologists, that this contribution from one of the foremost paleontologists of the continent is especially welcome.

Henry Fairfield Osborn.

March 3, 1908.

First Paper. Eocene Epoch

In a preceding contribution (*Comptes rendus,* 5 juin, 1905) upon the principles of evolution of the Tertiary mammals, I have enunciated the following general law: that when we attempt to establish the sequence of the forms which represent the evolution of a *natural phylum* we find ourselves, after tracing them backward through a geologic series of more or less length, almost always arrested by an impassable hiatus; this *apparent break* corresponds to the sudden appearance of the group under

[1] Extract from the *Comptes rendus des séances de l'Académie des Sciences,* t. CXLI, p. 702. (Séance du 6 novembre, 1905.) Translated by Johanna Kroeber.

consideration in the region of the globe which one is studying.

It is desirable to return to this general law of *faunal changes through migration* and to illustrate its interest more fully.

The importance of the migrations of terrestrial animals as correlated with great changes in the *paleogeography* of the continents, was fully recognized a century ago by Cuvier. The illustrious founder of paleontology had been justly impressed by the absence or rarity of forms of passage between the superposed fossil faunæ. Exaggerating somewhat, owing to the imperfect evidence before him, the consequences of this observed fact, Cuvier had deduced from it the renewal of faunæ *in toto* (after their destruction by *terrestrial cataclysms*) not by successive *creations,* as he is often accused of advocating, but by extensive *migrations* of animals foreign to the region. Since his time, many paleontologists, Wallace, Lydekker, Zittel, Schlosser, Gaudry, Osborn, Ameghino, etc., have given their attention to this subject and have reiterated its significance. It appears to me, however, that these contributions have been of too speculative a character, inadequately supported by precise data. It has resulted that the majority of the essays at the *genetic* or *structural phylogeny,* which have been attempted in various groups of fossil mammals, are defective, chiefly because their authors have almost always sought to find in place in the particular country which they inhabit the various evolutionary series of these groups.

No doubt there are great practical difficulties in refastening link to link the segments of the broken chain which forms the evolutionary series of each of the innumerable branches of the mammalia. Nevertheless, the obstacles are smoothed away by each new discovery; thus the recent disinterment of the Oligocene and Eocene of the Libyan desert, of the ancestors of the Proboscidea, the Mastodons and Dinotherium, which appear so suddenly in Europe at the beginning of the Miocene, and

whose origin has been until now an insoluble enigma, indicates the method we should follow, and the necessity for searching for the *centers of dispersion* of each branch.

A preliminary work at least is possible at our present stage of knowledge; it is to establish for each region whose paleontologic exploration is sufficiently advanced, the part which pertains to each of the two factors determining faunal changes: (1) *Evolution of the local fauna* (autochthonic evolution), (2) *Immigrations from a distant region.*

I shall attempt to analyze these facts for the Tertiary faunæ of Europe, where this distinction has never been established in a systematic manner.

I. *Thanetian* or *Lower Londinian* stage (deposits of la Fère, Cernay, Rilly, Châlons-sur-Vesle in France; of Erquelines in Belgium).

1. *Local Evolution.*—A single instance, *Neoplagiaulax* (Multituberculata), which may perhaps have been derived, in spite of the great gap of the Cretaceous, from *Plagiaulax* of the Purbeck, but may also have migrated from North America.

2. *Migrations of North American Origin.*—Introduction into Europe of several families of Creodonta: Oxyclænidæ (Procynictis = Chriacus), Arctocyonidæ (Conaspidotherium = Clænodon), Mesonychidæ (Dissacus); and of the Condylarthra (Euprotogonia).

3. Migrations of unknown origin of the Insectivora (Adapisoricidæ), of the (?) Artiodactyla (Pleuraspidotheriidæ), of the aberrant Primates of the group Plesiadapidæ, of the Perissodactyla (Hyracotheriidæ or Preequidæ), of the Amblypoda (Coryphodon).

II. *Sparnacian* or *Upper Londinian* stage (deposits of Soissons, Guny, Muirancourt, Saron near Ste Maxence, Laon, Upper Cernay, Meudon, Vaugirard, Sézanne, in France; Dulwich and Croyden (Woolwich beds) in England. Fauna unfortunately still very scanty.

1. *Local Evolution.*—Continuance of Amblypoda (Coryphodon, and of Hyracotheriidæ (? Pachynolophus).

2. *North American Migrations* of certain Creodonta (Pachyæna, Palæonictis).

III. *Lower Ypresian* stage (beds of the London Clay, Herne Bay, Kyson, Harwich, Isle of Sheppey, in England; beds of Pourcy near Reims in France). Fauna little different from that of the preceding stage.

1. *Local Evolution.*—Continuance of Amblypoda (Coryphodon), and of Hyracotheriidæ (Hyracotherium).

2. *Migration of North American Origin* of the Tillodontia (Platychærops = Esthonyx).

IV. *Upper Ypresian* stage (beds of Teredo-sands, Ay, Cuis, Chavot near Epernay).

1. *Local Evolution.*—Continuance of Insectivora (Adapisoriculus), of aberrant Primates (Plesiadapis), of Creodonta-Mesonychidæ (Hyænodictis = Dissacus), and of Hyracotheriidæ (Propachynolophus).

2. *Important Migrations, Probably of North American Origin,* of the mesodont Primates (Notharctidæ, genus Protoadapis), of the Rodentia-Pseudosciuridæ (Decticadapis), and Sciuridæ (Plesiarctomys), of Lophiodontidæ (parallel branches Lophiodon and Chasmotherium), of the Paridigitate Suillines (Protodichobune) and perhaps of Titanotheridæ (Brachydiastematotherium).

This horizon is marked by some important migrations and great changes in the mammalian fauna, in consequence of which the latter approximate more closely to the fauna of the middle, than to that of the lower Eocene.

V. *Lutetian* stage, two successive faunæ:

(*a*) *Lower* and *middle Lutetian* (beds of Argenton, of Bracklesham and part of the "terrain sidérolithique" of Egerkingen and of Lissieu).

Local evolution of Lophiodontidæ (Lophiodon, Chasmotherium), of Hyracotheriidæ (Pachynolophus, Propalæotherium) and of Dichobunidæ (Meniscodon, Dichobune).

(*b*) *Upper Lutetian* ("Calcaire grossier" beds of Paris: Nanterre, Vaugirard, Gentilly; Coucy, Dampleix; of Buschweiler, of Issel; les Matelles, St. Gily du Tesc;

the larger part of the "terrain sidérolithique" of Egerkingen and of Lissieu).

1. *Local Evolution.*—Continuance of Lophiodontidæ (Lophiodon, Chasmotherium), of Hyracotheriidæ (Pachynolophus, Propalæotherium, and intermediate forms leading to Lophiotherium), of Creodonta-Oxyclænidæ (Proviverra), of Rodentia-Sciuridæ (Plesiarctomys), of Dichobunidæ (Dichobune, Mouillacitherium), and of the mesodont Primates (Cænopithecus, ? Adapis).

2. *Important Migrations of Unknown Origin* of the Palæotheriidæ (appearing suddenly with their two branches Palæotherium and Plagiolophus), the Anchilophidæ (Anchilophus), the Suidæ (Chœromorus, Acotherulum), the Anthracotheriidæ (Catodontherium n. g., forerunner of Brachyodus), the Dacrytheridæ (Dacrytherium), the Xiphodontidæ (Xiphodontherium), the Dichodontidæ (Dichodon, Tetraselenodon, Haplomeryx), some Sciuridæ (Sciurus), the Talpidæ (Amphidozotherium), the Erinaceidæ (Neurogymnurus).

3. *North American Migrations* of the Hyænodontidæ and probably of the Lemuroidea-Anaptomorphidæ (Necrolemur).

VI. *Bartonian* stage (calcareous deposits of St. Ouen near Paris) of Sergy (Aisne), sandstones of Castrais (Lautrec, Mazou, Viviers, Montespien, etc.), of Robiac (Gard), "terrain sidérolithique" of Heidenheim and part of those of Mormont; very small part of the phosphorites of Quercy.

1. *Local Evolution.*—Continuance of Lophiodontidæ (last of Lophiodon and Chasmotherium), of Hyracotheriidæ (primitive representatives of Lophiotherium), of Palæotheriidæ (numerous parallel branches), of Anchilophidæ (Anchilophus), of Anthracotheriidæ (Catodontherium n. g.), of Suidæ (Chœromorus, Chœropotamus), of Xiphodontidæ (Xiphodontherium), of Creodonta (Hyænodon), of Sciuridæ (Plesiarctomys), of Adapidæ (Adapis).

2. *Migration, perhaps of North American Origin,* of the Chalicotheriidæ (Pernatherium).

VII. *Ludian* stage, two successive faunæ:

(*a*) *Lower Ludian* (deposits of Saint Hippolyte de Caton (Gard), of Hordwell (Isle of Wight), lower strata of the Gypse de Paris; part of the Quercy phosphorites.

1. *Local Evolution.*—Continuance of Palæotheriidæ, of Hyracotheriidæ (last of Lophiotherium), of Anchilophidæ, of Suidæ (Chœropotamus, Cebochœrus), of Dacrytheridæ (Dacrytherium), of Xiphodontidæ (Amphimeryx), of Dichodontidæ (last of Dichodon), of Anthracotheriidæ (Catodontherium), of Hyænodontidæ (Hyænodon, Quercytherium), of mesodont Primates (Adapis) and Anaptomorphidæ (Microchœrus).

2. No new migration known.

(*b*) *Upper Ludian* (Gypse de Montmartre, deposits of Gargas, of Mornoiron, of Villeneuve la Comptal; of the Bembridge beds and the Headon beds in England; part of the phosphorites.

1. *Local Evolution.*—Continuance of Palæotheriidæ, of Anchilophidæ (last of Anchilophus), of Xiphodontidæ (Amphimeryz, Xiphodon), of Dacrytheridæ (last of Dacrytherium), of Anthracotheriidæ (first representatives of Brachyodus, earliest Anthracotherium), of Suidæ (last of Acotherulum, Chœropotamus, and Cebochœrus), of Dichobunidæ (last of Dichobune), of Hyænodontidæ (Hyænodon, Pterodon), of Sciuridæ (Plesiarctomys, Sciurus), of Adapidæ (last of Adapis), of the Lemuroidea (last of Necrolemur).

2. *Migrations of Unknown Origin* of the Anoplotheridæ (Anoplotherium), of the Cænotheridæ (Oxacron = Hyœgulus), of the Canidæ (Cynodictis), of the Rodentia-Theridomyidæ (Theridomys), and Myoxidæ (Myoxus).

3. *American Migration* of the Marsupial Didelphyidæ (Peratherium).

(*To be continued.*)

ZOOLOGICAL PROGRESS[1]

PROFESSOR G. H. PARKER

HARVARD UNIVERSITY

THE chase, the domestication of animals, and the practise of animal sacrifice in religious ceremonies were all customs of primitive man that led to an acquaintance with animal structure and habit long before human knowledge could be said to be organized. In the early steps of this organization, what we now know as zoology was a part of natural history, but in the specialization of modern times zoology has grown to the dignity of an independent science with numerous subsciences. In fact modern specialization has gone so far that concern has been frequently expressed lest the natural unity of science be entirely lost sight of; but, in sketching the outline of zoological progress, I hope to show you that, so far as zoology is concerned, this fear is unfounded.

Any outline of the course of zoological progress must be somewhat in the nature of an inventory of zoological possessions, and I can not do better in beginning this brief survey than to call your attention at once to the real materials of zoological research. These are the individual animals, which, as you well know, are not immensely diverse, but show certain agreements whereby they may be arranged in groups whose members have similarity of form and habit and show the remarkable trait of producing new individuals of like kind. These natural groups or species afford a basis for a descriptive inventory of the animal kingdom, and the attainment of such a complete description has been perhaps one of the most persistent motives to zoological work.

Progress in this undertaking is indicated by the increase in the number of species described at each succes-

[1] An address delivered at The College of the City of New York.

sive period. Aristotle, who is usually regarded as the father of natural history and who lived in the fourth century B. C., mentioned in his zoological treatises about 480 kinds of animals. Linnæus, in the tenth edition of his "Systema Naturæ," published in 1758, described 4,378 species. Günther estimated that in 1830 a total of 73,588 species had been reached and that in 1881 the number had mounted to 311,653. Sharp placed the total in 1896 at 386,000, and, judging from the rate of increase in the vertebrates and echinoderms, the total number of described species at present must be approximately 500,000. From these estimates, which include only living species, it must be clear that in the twenty-two centuries between Aristotle and Linnæus the number of species known to the naturalist had increased only ten-fold, while in less than a century and a half after Linnæus the increase had been over a hundred-fold.

This enormous increase has been the result of two processes: the actual discovery of new forms in nature and the subdivision of what was originally regarded as one species into two or more species. The actual discovery of new forms implies the gradual exhaustion of nature and the conclusion of this process will come when exploration can yield no more new species. That the naturalist even of to-day is far from this goal is only too well known and can be illustrated by the following instances.

All of you doubtless have seen a delicate pearly shell, chambered somewhat like a miniature nautilus, but with its whorls open. This shell, which is known as the Spirula, is found commonly on the shores of the tropical oceans and may even reach our more northern coasts. It is extremely fragile and hence it can not last long on a surf-beaten shore. Nevertheless it is sometimes so abundant on tropical beaches as to form veritable windrows. Each shell is the life product of a single Spirula animal, which, so far as one can judge from the abundance of shells, must be a common inhabitant of the tropical seas. And yet, aside from fragments, the Spirula animals thus

far obtained number only six. The first was collected in New Zealand and dissected by Sir Richard Owen. The second, for which no locality is known, was purchased by the British Museum from a dealer and dissected also by Owen. The third was collected near Port Jackson, Australia, and is now preserved in the Sydney Museum. The fourth was dredged near New Guinea by the "Challenger" and was studied by Huxley and Pelseneer. The fifth was taken by the dredge in the West Indies by the United States steamer "Blake," and the sixth was caught near Sumatra in a deep-sea net by the German expedition on the "Valdivia." If an animal as common as the Spirula must be, is known only by some six specimens, what a host of rare and undescribed species the ocean must contain.

Not only are the ocean basins treasure stores of undescribed species, but the land areas are also far from exhausted. It would seem fair to have presumed that of the terrestrial quadrupeds certainly all the larger and more striking species had been described, and yet, since the opening of the new century, a large cloven-hoofed mammal in general appearance somewhat between a donkey and a giraffe has been discovered in the Semliki forests of central Africa. This remarkable mammal was sought for in 1900, at first unsuccessfully, by Sir Harry Johnston, who finally succeeded in obtaining a skin and a skull from which the animal was described by Lankester in 1902. The natives call it okapi and report it by no means rare, and yet it remained almost to the present time without being known to science. But the naturalist is not obliged to search the deep sea or to journey to central Africa for new species. There is hardly an order of insects that could not be enriched with new forms by a season's collecting even within the limits of New York City, and it must therefore be evident that the half-million of species now described is only the beginning in the inventory of nature's stores.

In addition to the discovery of new species in nature,

the process of splitting what was assumed by the older zoologists to be a valid species into two or more new ones has also considerably increased the number of described forms. This practise, though sometimes questionable, is at least illuminating, for it raises at once the fundamental question of what constitutes a species. In the days of Linnæus when special creation was more generally adhered to than now, it was comparatively easy to meet this question by the statement that a species is the aggregate of individuals represented by the originally created pair or stock and their descendants; but, with the acceptance of the evolutionary idea, this reply no longer sufficed. From the evolutionary standpoint every species has had a history and this history has been clearly one of change whereby the aggregate of more or less similar individuals at one time representing the species gave rise to the self-perpetuating stock whose more remote members evolved in one or more directions new features, so that the species either as a whole assumed new characteristics or split into two or more subordinate groups, each having its own special features and being destined eventually to become as well circumscribed from its next of kin as the original stock was at the outset. With this process in mind it is fair to expect that nature would be found to embrace many aggregates of individuals which would represent species at all steps of differentiation, and whether the individuals of a given aggregate had come to differ sufficiently among themselves to constitute a new species or not would depend entirely on the judgment of the naturalist who described them. It is thus clear that we can not expect any fundamental characteristic by which a new species can be definitely determined, for it is obvious that the transformation of species is a more or less continuous process in which the degree of separation whereby the new species will be established is somewhat arbitrarily determined by each describer. Hence the idea of species rests upon an artificial basis, and, if the describer's measure of specific difference diminishes with the progress of

time, it is perfectly legitimate to subdivide previously described single species into smaller aggregates to be denominated new species.

Where this movement will lead to is not easy to foretell. It was hoped that the statistical methods of biometric work would make possible a solution of some of the difficulties in defining species, but, while these methods enable the investigator to discover and express differences between large groups of individuals vastly more accurately than the old methods of simple inspection and rough mental estimate did, they do not settle what characters or how many such shall be used in defining a species or what degree of difference must be arrived at before a given aggregate may be divided into two or more species. Nor does the recent proposition of de Vries come nearer to solving the problem. According to this investigator real species can be defined by a certain combination of characters which vary not in a continuous way but by leaps. These discontinuous variations constitute differences that may be as distinct as the differences between chemical elements; and any real or elementary species, as de Vries designates it, is distinguished by one or more of these elementary characters. Such elementary species, though open to variation, are cut off absolutely in their specific characters from other such species by a gulf that is never bridged by intermediate forms. Hence they ought to be as easily and distinctly describable as chemical compounds or even chemical elements. These elementary species, which have been for the most part heretofore ignored or passed over simply as races, etc., are the real units of systematic zoology and are much more numerous than the ordinary or Linnæan species. In fact, each Linnæan species probably consists of many elementary species and consequently the acceptance of this proposition would multiply the number of described species many times. But the difficulty with this proposal is to be found in the fact that an inspection of the so-called elementary characters shows them to be not so

stable as de Vries assumed. In some characters, like coat colors, fixity is more or less realized; but in other features, particularly dimensional ones, such an amount of variation is shown that the resulting forms necessitate the same artificial methods of separation as those to which the older systematists were obliged to resort. From a radical standpoint there seems to be no escape from the view that a species is at best an imperfectly definable aggregate of more or less similar individuals and that this conception rests upon an artificial basis.

Although the idea of species must be admitted to be artificial rather than natural, its immense practical importance is not to be lost sight of; for, as a tool in the hands of the working zoologist, it is absolutely indispensable. Moreover, the arrangement of species into related groups and the development thereby of a system of classification has led to views on animal phylogeny of the utmost significance. That living animals range from the relatively simple unicellular protozoans to the immensely complex vertebrates suggests at once that the modern faunas include not only the latest products of animal evolution but many remnants of the remote past. This state of affairs is a continual temptation to picture the past history of the animal kingdom in terms of modern forms and to assume, for instance, that the protozoans of to-day are like the primitive protozoans from which the higher animals have been derived. This attitude leads to the discussion of the so-called affinities of the modern groups, a practise that in my opinion is open to the objection of attempting to make parents and grandparents out of brothers and sisters. How futile this practise is can be seen in such a group as the reptiles. You are doubtless aware that the modern reptiles are included in four orders: the chelonians, or turtles; the crocodilia; the rhynchocephalia, represented by a lizard-like reptile from New Zealand; and the squamata, or lizards and snakes. You are probably not so well aware that the class of reptiles also includes five other orders, all fossil, among

which are to be found some of most specialized and prodigious land and water animals known. No possible consideration of the recent orders of reptiles would ever lead one to suspect the remarkable nature of these ancient forms, and the so-called affinities of the recent orders become meaningless in the light of the true ancestral relations as seen in the past history of the group as a whole. Tempting as the field of speculative phylogeny is, its results can never be of much value till they receive the endorsement of actual history as traced in fossil ancestry. In this connection I can not do better than quote a short passage from Huxley, who, as you well know, was an ardent student of fossil as well as living animals. In his essay on "The Advance of Science" he says:

> A classification which shall represent the process of ancestral evolution is, in fact, the end which the labors of the philosophical taxonomist must keep in view. But it is an end which cannot be attained until the progress of palæontology has given us far more insight than we yet possess into the historical facts of the case.

It is plain that the history of the animal kingdom is to be sought for not through ingenious speculations on the recent groups of animals, but by the persistent and patient exploration of the fossil-bearing rocks.

Although the study of animal genealogy, as outlined by fossil remains, is a relatively novel field, it has already yielded certain general results worthy of careful attention. It is customary at present to group all species of animals under some ten or twelve main divisions or phyla of the animal kingdom. These phyla have doubtless been evolved from some common group of animals in the remote past, and consequently, in tracing back their history as represented by fossil forms, it is not unreasonable to expect that their lines would gradually converge toward this common ancestral stock. In some instances, like the flat-worms, the phylum is known only through its modern representatives, and these representatives are of such consistency that it is not surprising that none of these animals have been preserved in the fossil state. But,

aside from cases of this kind, all phyla that might be represented by fossils are, as a matter of fact, so represented; and the remarkable feature of this representation is that it does not show a convergence toward a common stock, but the phyla as such were as distinct in these early times as they are to-day. This state of affairs, which at first sight seems contrary to the evolutionary idea, is due in all probability to a universal destruction by extensive rock metamorphosis of the earliest of animal remains, and we are therefore probably correct in concluding that fossils at best give us only the later chapters in the evolution of the animal kingdom. Within a phylum the main lines of descent can sometimes be clearly discerned, but between phyla there are no absolutely certain connections, nor is there as a matter of fact a single completely extinct phylum known. These facts lead us to see that for an immensely long period the main divisions of the animal kingdom have been as they are at present and that the genetic connections of the phyla, which would be discernible with certainty only through their fossil remains, are, in consequence of the absence of these, probably absolutely and irrecoverably lost. Even the important suggestions that embryology has yielded as to the phylogenetic relations of the chief animal groups must remain forever hypotheses because of this irreparable blotting out of past records.

Although the systematic zoologist may look upon the animal kingdom as composed of imperfectly definable aggregates of individuals whose relations in the remote past are irretrievably lost but whose numbers are such as to occupy his labors for many years to come, his arrival at this conception has been over a course that has brought to view such a multitude of new prospects that the real extent of zoology is only now beginning to be dimly seen. These more recently acquired territories, which are now being cultivated with a vigor no less than that bestowed in past times almost exclusively on systematic zoology, must now be looked into. It is somewhat difficult for us

to conceive of the state of mind of the zoologist of a century ago so far as his conception of the structure of animals is concerned. To him they consisted of organs composed of a variety of unrelated substances, such as muscle, membrane, bone, fat, blood, etc., which constituted the elementary materials of the animal body. It was therefore a great step forward when Schwann showed in 1839 that animals, like plants, were composed of structural units or cells whose physiological significance, as Brücke afterwards pointed out, entitled them to the name of elementary organisms. Many lower animals, belonging to what are now called the Protozoa, proved to be single cells, while the higher animals in all cases were found to be multicellular. The number of cells entering into the formation of the body of one of these higher animals is truly enormous. It is impossible to get reliable statements for these numbers in any single complex animal, but a recent careful estimate of the number of ganglion cells in the human cerebral cortex places the total at 9,200,000. As this enormous number of cells would occupy less than a cubic inch of space, one can form some rude conception of the prodigious number in the whole human body.

It is a remarkable fact that almost all cells, whether they are whole single animals or only parts of animals, are of small size. There seems to be something about the organization of a cell which ordinarily prevents it from enlarging much beyond microscopic proportions. The essential parts of a cell are its nucleus and the surrounding cytoplasm, and the continued activity of the cytoplasm is known to be dependent upon the presence and integrity of the nucleus. Such being the case it would seem as though the nucleus could administer to only a limited volume of cytoplasm and thus restricts the size of the cell. Apparently, however, this relation is one of volume and not of distance from the nucleus, for the cytoplasm of a ganglion cell may be drawn out into a most delicate nerve-fiber process that may reach half the length of the human body.

The arrangement of the cells in the body of a multicellular animal is not, as in most plants, of a more or less promiscuous kind, but conforms to certain fundamental principles. Among these probably the most important is one that depends upon the fact that animals assimilate solid food. To carry out this operation they possess almost universally a digestive cavity into which this solid food is carried and there rendered soluble. The only multicellular animals that do not possess a digestive cavity are certain parasites, like the tapeworm, whose modes of life are such as to make digestive organs superfluous. In the simpler multicellular forms, the coral animals, etc., the whole animal is sac-like in structure and may be briefly described as an animated stomach. Not only is this state characteristic of such primitive forms, but in the development of almost every multicellular animal known, the first organ to be formed is the digestive organ. This is brought about in that the cells, which are destined for the future animal's body, become arranged in the form of a two-layered sac in which the inner layer or entoderm bounds the digestive space and the outer one or ectoderm acts as a protective covering. Both layers develop a certain amount of muscular tissue and this is brought into action through external stimuli that from the nature of the case are received usually by the ectoderm. Hence this layer becomes the seat of those changes which in the higher animals eventually shape themselves in the sensory and nervous organization of these forms, while the entoderm is concerned with the digestive functions. Between these two layers there develops in all the higher multicellular animals a third layer, the mesoderm, which, as has been intimated, is primarily muscular in character but may also give rise to the internal skeleton, circulatory system, and other related sets of organs. Thus the body of a multicellular animal is composed of definite layers or masses of cells, chiefly three in number, with which special functions or modes of activity have become firmly associated.

Although these cell layers as such retain their limits in a most striking and clear way in the bodies of the higher animals, they must not be thought of as independent or in any sense isolated in their development. Their mutual relations are often of a most intimate kind and in the course of their development these relations tend rather to become more firmly consolidated than the reverse. This condition is well illustrated by the growth of the neuro-muscular mechanism in animals, a growth that can be traced step by step through the multicellular forms till it finally shapes itself into the complex machinery whereby the animal reflexes are carried out.

The first step in this process is seen in the sponges, which in some respects are the simplest of the multicellular animals. As is well known, these animals are quite as sluggishly responsive to stimulation as plants are. A long and unsuccessful search for their nervous organs has ended in the belief that they possess no such structures. Some of their cells, particularly in the neighborhood of their numerous pores, are elongated or even fibrous and are apparently contractile enough to serve as a means of closing these openings. It is highly probable that these contractile cells, which may be regarded as primitive muscle cells, are brought into action by some stimulus directly applied to them, such as dissolved materials in the sea-water, etc. We are so accustomed to think of muscle as controlled by nerve that independent action of this kind seems wholly anomalous. And yet it must not be forgotten that muscle can be made to contract by the direct application of a stimulus and that even in the higher animals under natural conditions this may occur. Steinach has shown that when bright light is thrown on the eye of a fish or an amphibian the pupil will contract even after all vestiges of nervous connections have been destroyed, and he believes this to be due to the direct stimulation of the muscle fibers by light. This case supports the opinion that in sponges the contractile tissue responds to direct stimulation, and in my opinion the

sponge represents the first step in the differentiation of the neuro-muscular mechanism, a step in which the primary and fundamental character of muscle is disclosed in that this is the only constituent present. This self-sufficiency of muscle is also made evident in the rhythmic beat of the embryonic chick heart before nervous differentiation has taken place.

In the sponges the primitive muscle cells lie either in the ectoderm or the subjacent mesoderm. In the coral animals, the jellyfishes, and their allies, the muscle cells occur in the deeper parts of the ectoderm and entoderm, a position where a forming mesoderm might be expected. It is usually stated that in the higher animals the muscles are derived from the mesoderm, and in individual development this is true, but from a phylogenetic standpoint I believe the reverse to be the case, namely, that the mesoderm has come from muscle and that the first step in the real origin of this layer is indicated in the migration of the muscular tissue of the cœlenterates or other like forms from the ectoderm or entoderm into the region between these two layers. This operation, which involves both layers in many of the lower animals, is usually limited in the higher forms to the entoderm, probably because this layer is the one which by reason of its proximity to the digestive cavity can best supply material for future growth. But, however this may be, it seems to me probable that the mesoderm has had its origin in the process of muscle formation, a process that is seen in its incipiency in the cœlenterates. That the mesoderm is also concerned with providing mechanical support for the animal is obvious, but in my opinion its contractile function is the primary one.

It cannot be stated with certainty at present that in the normal action of cœlenterate muscle this tissue is stimulated directly, though the investigations of Loeb on the jellyfish, Gcnionemus, show beyond a doubt that such a method of stimulation is possible. It is, however, well established that in many jellyfishes muscle action is

under the influence, if not the control, of nerves, and these cases represent, so to speak, the second step in the differentiation of a neuro-muscular mechanism. In such jellyfishes, groups of cells especially open to stimulation by light, pressure, etc., occur on the edge of the bell, and from these sense bodies nerve fibers pass to the muscular sheet on the under face of the bell. These sense bodies evidently act as triggers by which the muscular mechanism can be brought into action and in that way render it more delicately responsive than if it relied entirely upon direct stimulation. The relation of such a system may be described as that of a set of sense organs directly connected with a musculature, for there is nothing here that can be fairly described as a central nervous organ. As the sense organs are in the ectoderm and the muscles represent incipient mesoderm, it is obvious that the future development of these two layers will in this respect be most intimately bound together.

The last organ, in my opinion, to appear in this chain of development is the central nervous organ, the brain and its subordinate centers. This originated on the line of connection between the sense organ and the muscle, but rather from the sensory than the muscular end, as is shown by its anatomical relations in adult animals and by its invariable origin in the embryo from the ectoderm. It is scarcely recognizable in the simple multicellular animals and begins to be an obvious organ in such intermediate forms as the worms. Here it serves chiefly as a means of freer and more extended communication between the sense organs on the one hand and the musculature on the other, and thus lays the foundation for the marvelous development that it shows in the higher animals, where, as a storehouse of race and individual experience, its significance is unparalleled. The paramount importance of the brain in fact is so fully recognized that it is usual to treat the sense organs as appendages of it, but, if the view that I have advanced is correct, just the reverse is true; the sense organs of a bilaterally symmetrical animal

are clustered at its anterior end not because the brain is there but because this is the end of the animal most likely to receive stimuli, and the brain is at this end because it has developed from this sensory equipment. The brain, in other words, is the appendage of the sense organs.

In tracing thus the growth of the three elements of the neuro-muscular mechanism, the muscle, sense organ, and brain, I have endeavored to keep before you their relations to those primitive organs, the ectodermic and entodermic cell layers, and to make clear to you how these cell layers come to be part and parcel of this growth. This subject might have been illustrated by any other set of organs than those concerned with the neuro-muscular mechanism; thus it is well known that the skeleton has been differentiated chiefly under the influence of the muscles, and that the digestive apparatus is as intimately associated with the differentiation of the circulatory organs as these are with the respiratory and excretory systems. But to discuss such relations even in a brief way would trespass too much on our present time, and I must therefore pass them by. Suffice it to say that in the main these relations constitute that province of zoology called by Goethe morphology, which includes the fundamental aspects of the form of adult and developing animals and which has been a field that for a century past has elicited the keenest interest from some of the most profound masters of zoology.

No one who has become deeply interested in morphological problems can have proceeded far without frequently meeting questions of a physiological nature. To answer these the simple observational methods of the past are insufficient, and it is necessary to resort to experimental procedure such as has been for a long time the practice of chemists and physicists. From this standpoint one enters what may be regarded as the most recent field of zoological research. Since the elementary substances of the animal body are the same as those of the inorganic world and since the stream of energy flowing

through that body conforms in large measure to principles already discovered in the physical and chemical laboratories, it has been generally assumed that the life processes of an animal are nothing more than complex examples of physico-chemical interaction. This idea has proved most stimulating in its effect on research, but to what extent it will be found true can not at present be stated. It is quite possible that the chemist and physicist have as much of a fundamental nature to learn from living material as they have already gained from lifeless substance.

The paramount influence of material in animal reactions can not better be illustrated than in such processes as inheritance. It is well known to you how much more closely on the average offspring resemble their parents than they do other members of their own species, and you are familiar with the long persistence of certain family traits. These resemblances are explained by the fact that the offspring start from a certain amount of living substance contributed by each parent, but the powerfully determinative qualities of this substance are only to be appreciated in certain cases. It is well known that in human beings there are two classes of twins, identical twins and ordinary twins. The latter come from two separate eggs and may vary as much from each other as any two members of the same family. The former come from a single egg which by some accident has become separated into two parts. Identical twins are always of the same sex and are often so alike in features and actions that they are almost indistinguishable even to their near associates. Their close similarity, which may amount almost to identity, shows that the substance from which they both came has developed in a most rigidly uniform way and indicates that the development of ordinary twins, as well as of other individuals, is probably also closely limited from the beginning, but the degree of this limitation is not discoverable in these cases, for we have no basis of comparison. Since living material can thus duplicate

itself in product, its significance in inheritance can not well be overestimated.

Not only may physical features be accurately inherited, but the capacity to perform various complex sets of actions may be transmitted with great precision. It is difficult if not impossible for us to state the exact source of many of our modes of actions. We inherit much and we learn much, and whether in a given complex act we are dealing with an inheritance or a new acquisition or a mixture is not always easy to state. With certain lower animals this question is perhaps more readily decided. Bees have the capacity of building a truly wonderful structure, the comb, which, because of economy of material and accuracy of workmanship, has long been an object of admiration. Is this complex activity inherited or learned by imitation? To answer this question, Kogevnikov reared some bees from a comb placed in an empty hive. After the bees had hatched and got their strength they proceeded without having seen other bees at work to make a comb that was as perfect as one made under ordinary circumstances. It might be objected that they had seen the comb from which they themselves had hatched, and this must be admitted to be so; but this fact is probably without significance, for they made perfectly typical queen cells the like of which they had never before seen. It is thus evident that not only structural peculiarities but highly complex activities can be inherited.

The means of this inheritance has already in a measure been made out. When a common protozoan, like Paramecium, reproduces, the parent body divides into approximate halves. Each of the two offspring receives not only a large portion of the parental substance but a certain number of cilia and other parts directly from the parent, and hence that the offspring should resemble the parent is not very surprising. When, however, reproduction in the higher multicellular animals is examined a somewhat different condition is discovered. Sexual reproduction is accomplished by means of a fertilized egg,

which consists of a mass of cytoplasm chiefly from the maternal side, a centrosome from the paternal side, and usually an equal number of chromosomes from each side. As the offspring may resemble both father and mother, it follows that the substance that is the vehicle of inheritance is very probably the material of the chromosomes, the chromatin. This chromatin carries from parent to child not the vestige of an organ and is inconceivably small in amount. The human egg cell is approximately a sphere with a diameter of about 0.2 of a millimeter, and with a specific gravity about that of water; consequently its weight is about 0.004 of a milligram. The volume of the chromatin of a fertilized mouse egg, as measured for me by Mr. J. A. Long, is somewhat less than one-thousandth of the volume of the whole egg, and, assuming that this proportion holds for the human egg, and that its chromatin has about the same specific gravity as water, the weight of this chromatin would be about 0.000,004 of a milligram. Yet this mere trace of material can influence the adult substance of two identical twins to such an extent that their bodily configuration and actions are scarcely distinguishable. If we estimate their combined weights to be 130 kilograms, the chromatin of the egg from which they came can be said to have influenced in this profound way 32,500,000,000,000 times its original weight. Of course it must be borne in mind that the chromatin of the egg is living and that in the growth of the individual it assimilates and thereby increases in volume; the chromatin is not spread through the growing body in ever-increasing dilution. But, even granting this, its precision in the transmission of characteristics is certainly most remarkable; for when it is derived from a single source, as in identical twins, its effect upon the growth of the two individuals is to make them most strikingly alike. It is important to observe that the chromatin of at least certain male cells is composed very largely of nucleic acids, and that it is therefore very probable that the chemical composition and structure of

these substances are intimately concerned with heredity. This discussion makes clear how extremely important certain materials are to the body and yet how impossible it is at this stage of scientific progress to frame any clear and consistent conception of the method by which these materials exert their influences.

If such relatively simple physiological questions as this concerning the material basis of heredity meet with difficulties such as I have pointed out, how vastly more intricate and perplexing must be the problem of the relation of the living materials of animals' bodies to their nervous and mental states. That such a relation exists is well recognized, but what this relation is will probably require many years even to outline.

It is in the direction of comparative physiology that the more important new advances in zoology are to be made. In my opinion zoology will meet with an expansion in this century quite as much as the study of electricity has in the last hundred years. When Franklin tried his hazardous experiment with lightning, no one suspected that he was dealing with a factor that could come to be of such paramount importance in every-day affairs as electricity has become, and it seems to me probable that the zoologist of to-day is working obscurely with problems that will eventually lead to revolutionary results. I have already pointed out the importance of certain minute quantities of material in inheritance, and the significance of this in animal breeding and in social problems must be evident. But in a thousand other ways the doings of animals are worthy of closest attention. Many of the most difficult problems that the human race has attacked have already found their solution among the lower animals. Secure aerial transportation, which is almost a dream with us, is an accomplished fact among many animals. Our own efforts are not so safe if they are more extensive than those of a flying fish. They are, however, by no means equal to those of a bat or an insect, and they are immensely inferior to those of a bird. Our

systems of artificial illumination are regarded by us as one of the many evidences of advanced civilization and yet our best products are ridiculously poor compared with those of the lower animals. Gas or other such luminants yield at best something less than one per cent. light, the remainder of the energy being dissipated as waste heat, and our most successful means of illumination scarcely reach fifty per cent. of efficiency. The radiant energy of the luminous organ of a fire-fly is all light, and none is wasted as heat. Were the processes of this organ understood and made applicable to daily life, they would at once sweep out of existence every illuminating plant known. Such a revolution as this suggests awaits only the advance of zoological science, and, as I have said, this may be looked for in the near future. To my mind it affords one of the brightest outlooks for zoological investigation.

Thus far I have scarcely touched on what has been for so long a time the rallying word in biological work, evolution. But, if we knew the physiological workings of the animal body, especially in relation to inheritance, etc., evolution would be in large part understood and the lines of work that have just been recalled would be only examples of evolutionary processes. The most promising recent change in the study of evolution, a change which we owe largely to de Vries, is the discovery that evolution as now understood is probably going on before our eyes and at a measurable rate; hence it is open to observational and experimental treatment and we may expect renewed and rapid growth in the near future for this line of work.

Many of the unexplored regions touched upon in this survey are of such magnitude that few can hope to be their conquerors, but all may aid in preparing the way. In invading these new regions former methods and means will be sure to be found insufficient; the help of kindred sciences, such as physics and chemistry, must be called upon. This appears to be a sufficient answer to those who thought that they saw in the subdivision of zoology and of other sciences a step away from the true unity of scientific endeavor.

NOTES AND LITERATURE

HEREDITY

The Possibility of Inheritance through the Placental Circulation instead of through the Germ Cells.—In the December issue of THE AMERICAN NATURALIST reference was made to Professor Bateson's explanation of the inheritance of hæmophilia. Hæmophilia is a tendency to excessive bleeding, ascribed either to "a peculiar frailty of the blood vessels or some peculiarity in the constitution of the blood." It is seen far more often in males than in females, yet the males do not transmit it. Physicians are so confident of this as to recommend that "the daughters should not marry as through them the tendency is propagated."

Professor Bateson compared the inheritance of hæmophilia with that of the horned condition in sheep. A hornless breed crossed with a horned form yields horned males and hornless females. The latter will transmit horns to their male offspring only, unless again crossed with horned stock, when horned females will also appear. This analogy with hæmophilia holds good in so far as the females transmit a condition which they do not present, and it suggests a possible explanation of the occasional manifestation of hæmophilia in females. It fails, however, in an essential point. The horned male sheep transmit their condition whereas the hæmophilic males do not.

A different explanation is suggested by the studies on immunity reviewed and supplemented by Dr. Theobald Smith.[1] Ehrlich, as he states, found that female mice which had been made immune to certain toxic substances gave birth to young which were also somewhat immune. The immunity was soon lost and was never transmitted to the second generation. Immune males did not transmit any immunity to their offspring. Other investigators, using rabbits and guinea-pigs, have shown the transmission of several forms of immunity through the females only.

The artificial immunity may perhaps be permanent in the parent guinea-pigs. It has lasted long enough to affect four litters of one female, and Smith has records of "a considerable

[1] Smith, T. The degree and duration of passive immunity to diphtheria toxin transmitted by immunized female guinea-pigs to their immediate offspring. *Jour. of Med. Research*, 1907, vol. 16, pp. 359–379.

number of guinea-pigs which transmitted immunity for over a year." One animal gave birth to a litter of immune young thirty months after receiving the immunizing injection. The immunity is not so well marked in the offspring, and Smith agrees with the general conclusion that the grandchildren of immunized females are never affected.

Ehrlich found that in mice lactation plays an important part in the transmission of immunity to offspring, and that normal offspring may gain a considerable degree of immunity by being nursed by immune mothers. This conclusion requires confirmation, for Vaillard and Remlinger agree that, in guinea-pigs and rabbits, nursing from an immune mother does not confer immunity.[2] Rosenau and Anderson[3] were able to exclude the milk as a factor in transmitting hypersusceptibility to serum injections by a series of "exchange experiments." In these experiments the offspring of a susceptible mother are given, immediately after birth, to a non-susceptible guinea-pig to nurse, and the young of the non-susceptible guinea-pig are placed with the susceptible mother. "From these exchange experiments we learn that the hypersusceptibility is not transmitted to the young in the milk."

Gay and Southard[4] believe that the well-known susceptibility of guinea-pigs to a second dose of horse serum is due to an unisolated substance which they name *anaphylactin*. This is probably transmitted from the blood of the mother to that of her young through the placental circulation. It is contained in the serum of a guinea-pig two hundred and four days after the animal has been made susceptible by the first injection, and if from 1.5 to 2.5 c.c. of serum from such an animal are transferred to a normal guinea-pig, the latter becomes susceptible. However, a transfer of serum from the second guinea-pig to a third does not produce susceptibility and this result corresponds with the observation that artificial immunity is inherited only by the first generation.

It is possible that hæmophilia is due to an abnormal chemical composition of the blood, such as produces its manifestations in the male rather than the female, owing to differences in metabo-

[2] Cited by Smith, *loc. cit.*

[3] Rosenau, J., and Anderson, J. F. Further studies upon hypersusceptibility and immunity. *Journ. of Med. Research*, 1907, vol. 16, pp. 381–418.

[4] Gay, F. P., and Southard, E. E. On serum anaphylaxis in the guinea-pig. *Journ. of Med. Research*, 1907, vol. 16, pp. 143–180.

lism in the two sexes. If its cause is a substance in the blood it may be "inherited" from the female alone, and the male which manifests the disease can not transmit it. Thus it would be a case of transmission through somatic elements rather than through the germ cells.

F. T. L.

INVERTEBRATE MORPHOLOGY

Form Variation in Amblystoma tigrinum.—Powers[1] has observed the aquatic forms of this salamander both in their natural environment and under artificial conditions. His paper contains a large amount of material of great interest which would be much clearer reading if the numerous observations and experiments had been more explicitly described as to objective point and methods employed. The paper is too long for condensation here, but a few of the results can be noticed and will be welcome to those interested in the axolotl question. He distinguishes two main types, the ordinary larvæ and the cannibals, both by habits and in important points of structure. Taking the ordinary form first, two types as a body form are recognizable: those with the habit of crawling about on the bottom in a sluggish manner and thus living largely in the dark, these are of a broader shorter form and are called the "robust type," and a second type of quite different habit, being active swimmers going about actively in search of their prey, and of an elongate slender form, the "slender type." There is a great difference in the ratio of head width to total length in these two types, head width being contained 6.42 in total length in the robust type and 11 times in the slender ones. The mode of feeding is quite different in these two types. In the robust bottom-living forms food is obtained by using the mouth as a sieve and opening it widely to strain water through it in hopes of finding food thereby, with the result that the gape is increased. On the other hand, the slender swimming forms go about actively in search of prey, which, when they see it, they actively seize so that the mouth is not opened so widely as in the sieving process of the sluggish robust type. He also notes variations in special parts, such as the tail, the head and the posterior limb. Tails vary

[1] Powers, J. H., '07. Morphological Variations and its causes in *Amblystoma tigrinum*. Studies from the Zoological Laboratory of the University of Nebraska, 71, pp. 1–77, pls. i–ix.

from broad to narrow, long to short, some are flat and some more rounded and tapering, thick and fleshy or thin. Heads vary in breadth, length, thickness, contour of muzzle, distance between nares, between eyes, size of gape of mouth. Hind limbs vary as to robustness or slenderness, rounded or flattened shape of toes and habitual position of limb with reference to body. The writer of the paper is inclined to refer most of the variations which he finds directly or indirectly to the nutrition of the possessor. He says "excessive nutrition with these larvæ seems as it were to overflow into all the peripheral parts quite regardless of function." He shows very satisfactorily that the foot features which seem like aquatic life adaptations are not such in fact, but are due to over-nutrition. In swimming these forms do not use the foot; it lies idly alongside the body.

The cannibal form of larvæ is very interesting and wholly novel. There are occasional larvæ which for reasons as yet unknown, and against the tendencies of most of the larvæ, have adopted the habit of feeding on their fellows. It was possible to convert some non-cannibal larvæ to the habit, while not even starvation would induce others to adopt it. Cannibals, a number of photographs of which are shown, are characterized by the great over-development of the head and under-development of the body and tail. The changes came on rapidly after the habit had become established, a week showing very marked steps in that direction. The head enlargement includes internal as well as external anatomical changes, gill arches become more elongated, more numerous and much larger teeth develop in the palatine region; the entire head becomes more elongated, the brain more posterior in position, and, more strange still, it "is easily seen through the soft palate . . . and is of a less compact and more piscine type." All these points need fuller and more detailed description and illustration than is given in the paper, and will doubtless receive further attention in a later work.

The paper is a valuable contribution to knowledge of the variations of Amblystoma; it does not add to the interesting problem of the cause of the non-transformation of the aquatic forms. We do not find ourselves in accord with the author's proposition to consider this a dimorphic species having a terrestrial and an aquatic form, for this seems to put the aquatic form on a par with the terrestrial one. The aquatic form seems too

occasional in occurrence and locality to justify this. We do not know but that all aquatic cases would have metamorphosed under suitable conditions, and the terrestrial form is indicated as being definitive by the anatomy of the circulatory and respiratory apparatus. Also we do not share Powers's objection to the name axolotl and siredon as a designation for the aquatic form; both have the sanction of general usage and do not apply to other animals, so that they are entirely clear.

H. L. O.

EXPERIMENTAL ZOOLOGY

Some Experiments on the Development and Regeneration of the Eye and the Nasal Organ in Frog Embryos.[1]—Dr. E. T. Bell has conducted a series of experiments on embryos of *Rana esculenta* and *R. fusca,* in which he found certain new facts in the development of the eye and nasal organ. Wolff had shown in 1894 that the crystalline lens of the salamander may be regenerated from the upper margin of the iris. Fischel also found later that the lens in the newt's eye would regenerate from the iris, and by wounding the iris in several places after removal of the original lens that one or more lenses were formed. Spemann, Lewis and others show in amphibian embryos that there is no localization of lens-forming material in any given area of the ectoderm, and that the formation of a crystalline lens depends directly upon the stimulation of the ectoderm, or outer embryonic wall, through contact with the optic-cup. Lewis in a series of interesting experiments in which he tranferred the optic-cup from its original connection with the brain to a more caudal position showed that when it came in contact with the ectoderm in this new region the optic-cup stimulated lens formation. In another instance the skin from the ventral surface of *Rana sylvatica* was placed over the optic-cup of *R. palustris* and gave origin to a lens.

Bell has discovered several other possible sources of origin for the crystalline lens. He cut off the optic-vesicle of the embryo and turned it completely around so that the former outer side now turned toward the brain; under these conditions the pigment layer of the retina itself was induced to form a lens-like structure. When the brain was opened in the mid-

[1] *Archiv für Entwicklungsmechanik der Organismen,* XXIII, pp. 457–478, pl. 14 to 20.

dorsal line and the right optic-vesicle of another embryo of about the same size was put completely inside, the brain tissue, provided it had not become too far differentiated, gave rise to a lens. In another case a lens was formed from the surface ectoderm although the cavity of the optic-cup was turned away from the surface. An optic-vesicle which came in contact with the early nasal organ caused this structure to form a lens. Finally, the lens of one eye budded off another lens to supply an optic-vesicle which was placed adjacent to it. Bell's experiments seem to show that all ectoderm cells before becoming specialized to any considerable extent have the power to differentiate into lens cells, though all of his experiments are not equally convincing.

A lens failed to form from the endoderm when the gut was opened and the optic-vesicle turned down into its cavity.

King with the frog and Dragendorf with the chick have shown that the optic-vesicle may regenerate when parts of its early structure are removed. If, however, the eye-forming region be completely destroyed these authors claim that no regeneration takes place. Bell, on the other hand, finds that when one lateral half of the brain is removed it will regenerate and at times an optic-vesicle forms on the regenerated side. He also removed, by means of fine scissors, the entire Anlage of the eye and found a new optic-vesicle to regenerate. The previous experimenters used heated needles for destroying the eye and Bell believes that this method injures the adjacent tissue from which regeneration might take place.

The formation of the pigment layer of the retina, Bell claims, is dependent upon the retina proper. There is also some evidence to show that the retina may cause undifferentiated epithelium to become pigmented when brought into relation with it at the proper time.

Bell finds that the optic, as well as the olfactory nerve, may be induced to follow a path that can in no sense be preformed.

The olfactory lobes of the brain when brought into contact with ectoderm out of the nasal region are unable to stimulate the formation of nasal structures. The nasal anlage is readily regenerated if removed at certain stages and its early development is independent of the parts of the brain and buccal epithelium with which it normally connects. The nasal structure is developed from a predetermined area of ectoderm and when this portion of ectoderm is transplanted to a position

above and behind the eye the nasal pit still forms and the olfactory fibers which develop in it grow into the lateral wall of the diencephalon above the eye, which is of course an unusual region for these nerve fibers to enter.

C. R. STOCKARD.

The Influence of Regeneration on Moulting in Crustacea.—A recent paper by Dr. Margarete Zuelzer[1] furnishes additional data regarding the influences of regeneration, or the replacement of lost parts, on the moulting process in crustacea. It is generally known that the members of this group have the power to grow new appendages, legs, antennæ or swimmerets, after the former ones have been lost through accident or injury. In order to produce the new limb as well as to grow, or increase in body size, the crustacean must moult its hard chitinous shell. The processes of growth are closely associated with moulting and the more frequently the animal moults the faster will it increase in size. When one of these animals has lost a limb it is usually replaced by a small new one during the next moult following the injury.

Since the moulting period is so closely connected with the normal rate of growth several investigators have endeavored to ascertain what effect regeneration might have on the interval between these periods. Zeleny found that crayfish while regenerating their limbs moult faster, or more frequently, than normal individuals, and, further, he holds that an animal regenerating several limbs moults more frequently and regenerates the limbs faster than one replacing a single appendage. He concludes that during regeneration the moulting process is hastened. Emmel, on the other hand, has reached an opposite conclusion from the study of a large series of young lobsters. He finds normal individuals moulting more frequently than others which are regenerating new limbs. Lobsters that have lost several appendages moult slower than those that have lost fewer. Emmel, therefore, believes that regeneration retards the moulting process. He showed very clearly that an important factor, which Zeleny had failed to take into account, was the time at which regeneration was introduced into the moulting cycle. If the limbs were removed the day after moulting the moulting period remained almost normal, but when the limbs were removed four days after the moult the resulting regeneration

[1] Uber den Einfluss der Regeneration auf die Wachstumsgeschwindigkeit von *Asellus aquaticus* L. *Arch für Entwick.-Mech.*, XXV, Dec., 1907.

lengthened the interval before the next moult by eighteen percent. The longer the time intervening between a moult and the removal of appendages the longer the following moult was postponed through the influence of the resulting regeneration, although the less likely was regeneration to ensue.

Emmel's experiments also seem to show that the retarding influence is due to the regeneration phenomenon and not to the injury sustained, since in all of his experiments those animals that failed to regenerate new limbs did not have the moult following the operation postponed.

In the young lobsters the regeneration process retarded their growth at times more than twenty-four per cent.

Dr. Zuelzer, having the contradictory results of Zeleny and Emmel in mind, has undertaken a similar study on the little crustacean Asellus. Agreeing with Zeleny, she finds that in the majority of cases moulting occurs at shorter intervals if regeneration is taking place. The rapidity of moulting depends upon the time elapsing between the last moult and the time of operation, an important factor, as shown also by Emmel.

If the animal is operated upon during the moulting stage or shortly after, the following moult is usually hastened by the regeneration phenomenon. When more time intervenes between the moult and the amputation of the limbs the tendency is to delay the first moult following the operation, but to hasten the second and third moults. Should the amputation of appendages immediately precede a moult the moult occurs normally, but no regeneration is shown, the next moult is retarded and regeneration occurs; the third moult is accelerated and the regenerating limbs increased in size. Occasionally when the operation preceded the moult by a considerable interval no regeneration occurred, although the moult may have been hastened.

When the two antennæ are cut at different levels so as to leave stumps of unequal lengths, the longer one regenerates at a slower rate than the shorter, so that the original equality in length is again established. Zuelzer considers this a case of "compensatory regulation," that is, the short stump influenced the longer one to regenerate slower than it would otherwise have done in order to reestablish their equality in length. This difference in growth rates may be equally well explained as due to the levels at which the cuts were made on the two antennæ, as Morgan has shown for the fish's appendage that the nearer

the edge or tip of a fin the cut is made the slower will be the rate of growth of the new tissue.

Repeated amputation, or removal of regenerating buds, continues to accelerate the moulting process. Zeleny has shown in Cassiopea, a jelly-fish, that repeated operation also hastens the rate of regeneration. New tissue grows faster from a cut surface that has previously regenerated tissue than from a newly cut surface that has not before regenerated.

Zuelzer finds, like Emmel, that the moulting time is unaffected, or she believes at times hastened, in those cases where regeneration fails to follow the amputation of appendages. The reason for this she thinks may be that the animal with fewer appendages has a smaller body mass and, therefore, more food to use in normal growth, particularly when none of this food is used to form regenerating tissue. Thus Emmel's lobsters which failed to regenerate moulted more rapidly than regenerating ones. When one considers, however, the apparent unimportance of food-supply on regeneration phenomena as shown by Morgan he becomes disinclined to accept Zuelzer's explanation.

In a general way Zuelzer agrees with Zeleny in that regeneration hastens the moulting process. It is interesting to note that both of these workers have used adult crustacea while Emmel's experiments were made upon larval or young lobsters and gave opposite results. A possible reconciliation of the results may be as follows: The young lobsters, like most young animals, are growing at a maximum rate; all available energy is being used in growth. When such animals are injured they receive a "set-back" since some of their energy must now be diverted in order to repair the injury. Emmel showed that the process of regeneration retarded the rate of growth of these lobsters sometimes more than twenty-four per cent., but when the injury was not repaired growth or moulting was not retarded. Adult animals, on the other hand, are not living up to their maximum possibilities; they are in an apparent state of reserve until the removal of an appendage or other injury excites them to new activities and regenerative growth begins. During regeneration the animal may be said to be in a condition of newly stimulated growth and all growth activities are probably influenced. One may predict that if similar regeneration experiments be tried on the adult lobster the results will agree with those obtained on adult crayfish and Asellus.

C. R. STOCKARD.

Experiments in Transplanting Limbs and their Bearing upon the Problem of Development of Nerves.—Students of nerve regeneration are divided into two camps according as they view the influence of the central or ganglion cell on the regeneration of peripheral nerve fibers. On the one hand it is assumed that no regeneration can take place in peripheral nerves that are isolated from their ganglion cell. On the other hand it is assumed that regeneration can take place in the complete absence of central influence. This is often spoken of as "auto-regeneration."

The latter view finds its most recent exponent in Dr. Braus, of Heidelberg, who was led to it by the results obtained in transplantation experiments. He found that either the transplanted limb contained no nerves at all, or that functional nerves, typical in their distribution, were developed from any region of the body, whence they must have arisen *in situ* and secondarily come to unite with the ganglion cell.

A few details may be mentioned because of their extreme interest. Young tadpoles were used in which nerves had not penetrated to the limb buds. When such buds were transplanted to other regions of the body of a second tadpole, a limb developed in this bizarre position, quite normal in the structure of all of its parts, including its nerves. Posterior limb-buds were successfully grafted on the head, and posterior legs developed. As no nerves had been present in the buds at the time of transplantation, and as it seemed inconceivable to Braus that facial nerves, for example, could grow into the parasitic leg and show in the distribution of its parts an arrangement typical of normal limbs, he concluded that nerves must have developed *in situ.*

In a second series, the region which later gives rise to the nerve cells and fibers of the body was removed. Limb-buds from these "aneurogenic" individuals were grafted upon normal tadpoles and once again development of the limbs proceeded, but nerves were absent. If they grew centrifugally one should expect to find these limbs innervated by the outgrowing nerves from that particular region.

Professor R. G. Harrison, of Yale University, has rendered invaluable service in repeating and extending Braus's experiments, in a paper entitled "Experiments in Transplanting Limbs and their Bearing upon the Problem of Development of Nerves," in the *Journal of Experimental Zoology,* vol. 4, 1907.

In the first place, a careful examination of serial sections showed that nerves grow close to the region from which the transplanted buds were removed. The finer twigs of host and bud were thus brought into close union. It has been well established by a number of investigators that the union of the peripheral fiber of one nerve with the central fiber of another permits the functioning or regeneration of the former. This fact indeed is frequently taken advantage of in modern surgery. Similarly accurate examination of serial sections showed conclusively that, in the transplanted limbs taken from "aneurogenic" individuals, *nerves were present,* and that these were quite normal down to their minute details. There is thus presented the anomaly of a facial nerve, for example, growing along entirely new paths, whose direction is determined by the structures in the limb. Such distribution is thus not a function of the nerve, but of the organization of the limb which it innervates.

These more accurate methods revealed the further fact that accessory limbs, which are sometimes produced at the point of transplantation, also contain nerves often in a high degree of perfection. Braus had denied, on insufficient evidence, the presence of these nerves and had urged their absence as an argument opposed to their centrifugal growth.

By the aid of a very ingenious experiment, Harrison pushed the inquiry one step farther. "Aneurogenic" individuals, Braus and Harrison both found, were short lived. To overcome this difficulty, Harrison grafted an "aneurogenic" tadpole to the side of a normal or "nurse," and to the former he transplanted a limb-bud from a normal individual. A developing nerve was thus transplanted to a nerveless region. Though the results were not altogether satisfactory, the evidence pointed to the conclusion that "there is no progressive development of the nerve. On the contrary, there are rapid regressive changes, which in the majority of cases result in the entire disappearance of the nerves within a few days after they are cut off from their centers."

On the whole, though the paper is exceedingly accurate—a characteristic of Harrison's work—so far as it goes, it does not settle the question, especially in the light of Bethe's recent contribution. Perhaps, after all there is an element of truth on both sides, and just how much value to put to each is the problem to be decided.

A. J. G.

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